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AGE STUDIES ON THE FEMALE HUMPBACK WHALE, *MEGAPTERA NODOSA* (BONNATERRE), IN EAST AUSTRALIAN WATERS

By J. P. Robins*

[*Manuscript received July* 20, 1959]

Summary

Baleen plates, accumulated corpora albicantia, and cores of wax ear plugs are used as age determinants in this study of the female humpback whale. Baleen plates afford a measure of age for whales up to the 3+ age group, but above that age they are of limited use because of wear at the tip of the plate. The mean age at puberty, determined from baleen plates, is between 4 and 5 years. Observations on ear plugs and corpora albicantia from other whales show that this mean age occurs when 9·48 laminations have been laid down in the ear plug. For material collected in June to early September in the three seasons 1952–54 the average number of ovulations per whale was 1·13, but for the material collected in September alone in those seasons, the average number was 1·25. Assuming that two laminations per year are formed in the core of the wax ear plug it has been shown that the rate of accumulation of corpora in the ovaries is 1·10 per year. For several reasons this figure is considered to be too low and an alternative method of calculation indicates that an average rate of accumulation of 1·48 per year would be closer to the actual rate.

I. Introduction

It has been shown by several authors that the periodic growth differences shown in the baleen plates of balaenopterid whales may indicate their age. The suggestion that growth irregularities in the plates may indicate age was first made by Scoresby (1820), but his suggestion was not fully supported by Eschricht and Reinhardt (1866) although they showed that growth differences did occur in the plates. Wheeler (1930) unsuccessfully attempted to correlate age with number of ridges in the plate.

However, Ruud (1940, 1945) and Ruud, Jonsgård, and Ottestad (1950) showed that the periodic growth of the cortical layer of the baleen plate can be determined from the tracings of a machine and they assumed with supporting evidence that each period of two levels is equivalent to 1 year. These repeated variations in the thickness of the plates are ascribed to physiological changes due to the habit of periodic heavy feeding in the polar seas and non-feeding on the breeding grounds in tropical waters. The seasonal migration of humpback whales from polar to tropical waters is well known and the assumption that variations in thickness are due to the alternation of feeding and fasting periods appears to be a reasonable hypothesis.

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A second method of age determination used is that of Purves (1955) in which the core of the wax ear plug is used. The core secreted by papillae on the domed distal surface of the "glove finger" is composed of laminations which are assumed to be seasonal growth layers, the dark bands (keratinized zones) corresponding to the migration periods of which there are two per year (Laws and Purves 1956).

As corpora albicantia are considered to remain visible in the ovaries throughout the life of the whale (Mackintosh and Wheeler 1929; Laws 1958), relative age may be determined if the age of puberty and the rate of ovulation are known.

II. Material and Methods

Baleen plates from 62 individuals of the 148 humpbacks examined in the 1954 season on the east Australian coast were recorded as traces by use of a recording machine similar in construction to that described by Ruud (1940). The cores of wax plugs from 33 individuals of 101 taken during the 1956 season were examined. Of these 33 individuals, pairs of ovaries from 16 whales were available for study.

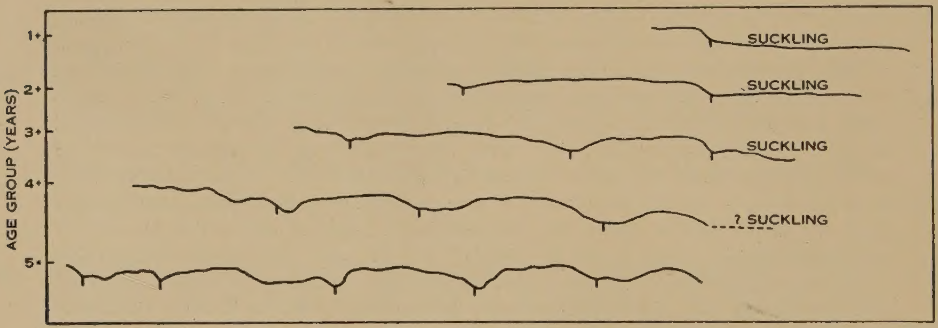

Fig. 1.—Representative baleen patterns of five age groups.

The ovaries from 309 mature and 73 sexually immature whales of a total of 519 whales caught during the 1952–54 seasons were examined and the number of ovulations experienced by each mature individual was determined. All whales were selected at random.

III. Age Determination

(a) *From Baleen Plates*

Tullberg (1883) showed that baleen development commenced at about 7 months in foetal life. In near-term humpback foetuses examined in eastern Australia, the longest plates protrude from the gum approximately 1½ in. and about 1½ in. lie below gumline level. Examination of the largest baleen plates from mature and juvenile humpback whales, captured over a 4-months period, indicates that in mature whales at least 3 in. and in juvenile whales up to 6 in. of the plate lie below the gumline. Based on the length of the last-formed full growth period which lies above the gumline, this hidden section probably corresponds to at least 6 months' growth and possibly longer (see below).

TABLE 1

DATA ON 62 FEMALE HUMPBACK WHALES FROM WHICH BALEEN PLATES WERE EXAMINED

Age Class	No. of Whales	No. at Puberty	Baleen Length (in.)		Whale Length (ft)		Av. No. of Corpora Albicantia	Immature (%)	Mature (%)	Puberal (%)
			Mean	Range	Mean	Range				
1+	2	0	13·88	12·00–15·75	32·37	30·25–34·50	0	100	0	0
2+	12	2	17·23	15·50–20·50	34·56	32·67–38·50	0	83	0	17
3+	20	3	19·34	17·50–22·50	38·04	35·33–39·92	0·15	65	20	15
4+	12	0	21·32	17·75–25·25	41·24	39·33–46·33	0·83	33	67	0
5+	7	1	23·32	21·00–24·75	41·46	38·92–43·66	5·00	0	86	14
6+	6	0	22·75	20·50–25·25	40·62	38·82–42·75	5·50	0	100	0
7+	3	0	27·75	25·50–29·00	44·30	43·00–46·25	6·00	0	100	0

Wear at the tip of the baleen plate limits its usefulness for age determination. In whales 4+ and older this method becomes unreliable because those sections of the plate which are recognizable in young whales as representing the foetal and suckling periods of life have been worn away. Again owing to individual variation in the rates of growth and wear of baleen the estimated ages of whales in groups 4+ and older are considered minimal.

Selected traces (Fig. 1) from each group are shown and it will be seen that as the whales age the increment in growth of the baleen decreases. From Tables 1 and 2 and Figures 2 and 3 which show the curves of apparent growth (i.e. total growth less wear), total growth, and wear of the baleen, it can be seen that an age is reached at which the amount of baleen added is equivalent to the amount worn away. This occurs from the 6+ group onwards and the average increases in baleen length for each period are 9, 9, 8, 7, 6, 5, 4, and 4 in. in the 0+ to 7+ age groups respectively.

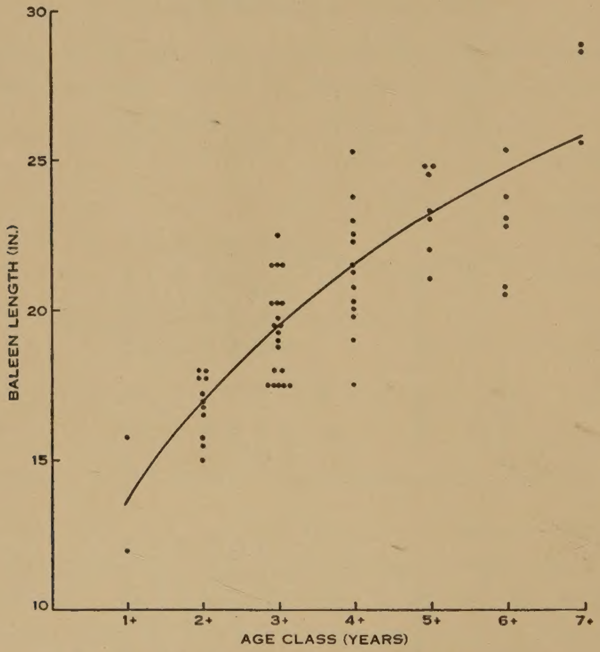

Fig. 2.—Apparent growth of baleen with age.

In Table 2 the apparent total growth in baleen length for each age group is shown. By adding the observed average growth for each successive year after birth, it is possible to determine the average total growth for each age group; the difference between accumulated growth and accumulated wear gives the apparent total growth for each group. However, it would appear that wear exceeds growth in groups older than 6+, and on ovarian evidence of accumulated corpora albicantia this must have occurred in the baleen of some of the whales classified in the groups 4+ and older. After this stage it would appear then that growth and wear are equivalent, for it is evident that if wear exceeded growth the apparent total growth would diminish as the whales aged.

Table 2 also shows that the average increment for each growing period exceeds the length of that part of the plate which, as previously mentioned, lies below the gumline and measures up to 6 in. in juveniles, and 3 in. in mature whales. This section could be equivalent to about 9 months' growth.

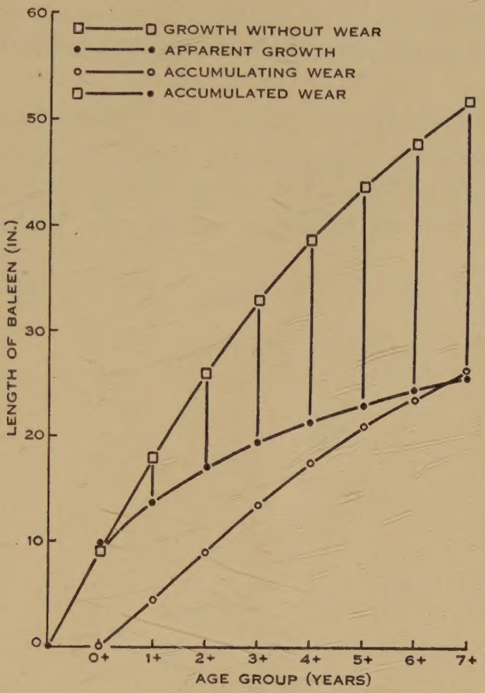

Fig. 3.—Growth and wear of baleen with age.

TABLE 2

CALCULATION OF GROWTH AND WEAR IN BALEEN

Growth Characteristic	0+	1+	2+	3+	4+	5+	6+	7+
Apparent total · growth (i.e. growth less wear)	–	13·75	17·00	19·50	21·50	23·00	24·50	25·75
Average increment for each period	9	9	8	7	6	5	4	4
Total growth (wear disregarded)	9	18	26	33	39	44	48	52
Cumulative wear	2*	4·25	9·0	13·50	17·50	21·00	23·50	26·25
Annual wear between successive groups	2·0*	4·75	4·50	4·00	3·50	2·50	2·75	
Apparent growth increment between successive groups	4·75	3·25	2·50	2·00	1·50	1·50	1·25	

* Pre-natal growth above gumline, 2 in.

Sexual maturity is attained by the majority of whales between the 3+ and 4+ age groups (Fig. 4), the first oestrous cycle (puberty) being determined by the occurrence of the first recently formed corpus luteum or a developing Graafian follicle 30 mm in diameter or larger (Chittleborough 1954). In this sample the age at which puberty is attained ranges from the 2+ to the 5+ age group.

(*b*) *From Rate of Accumulation of Corpora Lutea*

Age determined by this method, in which all ovulations previous to the season of killing of the whale are counted, is relative partly because the annual rate of accumulation varies between individual whales (see Tables 3, 4, and 5, and Section III(*c*)). The average age can be computed if the average age at puberty and the average annual increment of corpora lutea are known.

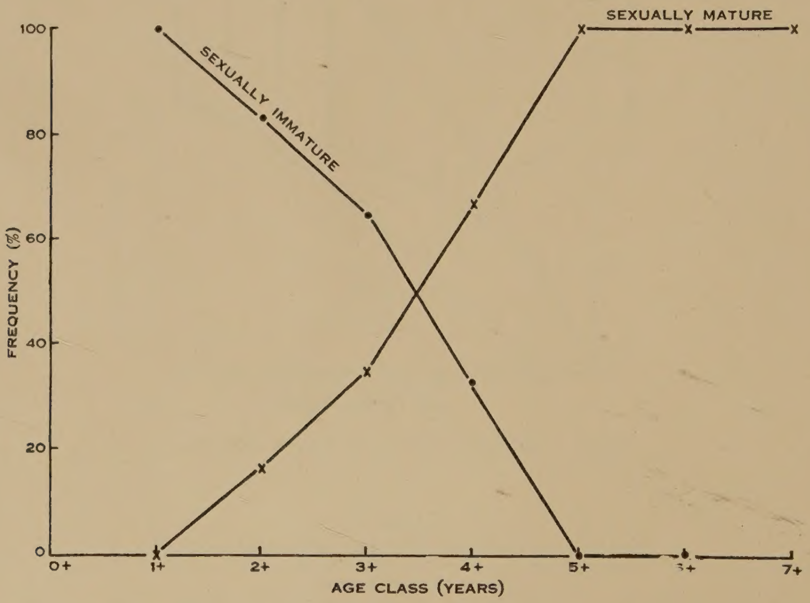

Fig. 4.—Percentage of sexually immature and mature whales, derived from baleen traces.

It was shown (Fig. 4) that puberty is attained in the majority of whales between the fourth and fifth years. Table 3 shows that the average number of ovulations for 60 puberal whales examined from July to September was 1·15, increasing from an average of 1·0 in July to 1·41 in September. Table 4 shows 309 mature whales (puberal whales included) in several phases of the reproductive cycle during the period June to September for the three seasons 1952–54. By calculation the rates of ovulation during this period in the breeding area are 1·13 excluding resting and late pregnant whales, 1·11 including resting whales which may have ovulated later in the season, and 1·10 including both resting and late pregnant whales which may have ovulated post partum.

The calculated rate for the month of September when no resting nor late pregnant females were examined is 1·25. Symons and Weston (1958) state that on the average 1·2 corpora are accumulated for every two laminations laid down in the wax ear plug.

It should be noted that examination of whales in eastern Australia was not made after the early weeks of September for the seasons shown in Tables 2 and 3. It is highly probable that the average rate of ovulation for the population as a whole would increase during October and November owing to the number of whales which were not successfully fertilized during their first oestrous period (see later), experiencing another oestrous period later in the season. Tables 3 and 4, and Figures 5 and 6, show an increasing rate from June to September, and Symons and Weston (1958) show that oestrous cycles occur in some individuals in late January or early February. The trend towards the polyoestrous state can be followed through from June to September. During the months of September (1952–54), of 69 whales examined it was found that 75·3 per cent. had ovulated once, 23·2 per cent. twice, and 1·5 per cent. three times, since the commencement of the ovulatory season in late June and early July. Based on the stage of development of the recently formed corpora lutea, the ovulations, in each particular whale examined, could not be considered to have occurred simultaneously. Laws (1958) suggests that the fin whale is seasonally monoestrous, but observations on the nature of the oestrous cycle in humpbacks show that in this species a significant percentage of the population

Table 3

ovulations observed in puberal whales (1952–54 seasons)

Year	Month	1 DGF*	1 RFCL†	1 RFCL+1 DGF	2 RFCL	Total
1952	June	—	—	—	—	—
	July	3	—	—	—	3
	Aug.	3	8	—	—	11
	Sept.	—	3	1	2	6
1953	July	1	—	—	—	1
	Aug.	2	12	1	—	15
	Sept.	3	3	2	—	8
1954	June	—	—	—	—	—
	July	2	3	—	—	5
	Aug.	1	6	1	—	8
	Sept.	—	1	1	1	3
1952–54	June	—	—	—	—	—
	July	6	3	—	—	9
	Aug.	6	26	2	—	34
	Sept.	3	7	4	3	17
	Total	15	36	6	3	60

* DGF = Developing Graafian follicle > 30 mm.

† RFCL = Recently formed corpus luteum.

experiences a polyoestrous cycle. Thus, if the average rate of accumulation of corpora albicantia is determined and the mean age at which puberty occurs is fixed, then a measure of relative age can be made for the sexually mature portion of the stock which has been sampled.

(c) *From Cores of Wax Ear Plugs and Corpora Albicantia*

The structure of the ear plugs in humpback whales conforms to the description given by Purves (1955) of the ear plugs of fin whales. The number of laminations can be determined in most core specimens although there is great variability in the intensity of colour of the dark-coloured laminations when cores from different whales are compared. Generally the colour is most intense towards the distal end of the core. Counts of the laminations, in a longitudinally bisected core, were made along the longitudinal axis and also along the horizontal axis at the base. Good agreement was found between the respective counts especially from cores with 16 laminations or less.

Table 4

OBSERVATIONS ON WHALES DURING VARIOUS PHASES OF THE REPRODUCTIVE CYCLE

Year	Month	1 DGF*	1 RFCL†	1 RFCL + 1 DGF	2 RFCL	2 RFCL + 1 DGF	Late Pregnant	Resting	No. of Whales
1952	June	3	—	—	—	—	—	5	8
	July	8	8	—	—	—	4	3	23
	Aug.	7	22	2	2	—	2	—	35
	Sept.	—	19	8	2	1	—	—	30
1953	July	4	4	2	—	—	2	—	12
	Aug.	7	48	2	1	—	5	2	65
	Sept.	3	21	4	—	—	—	—	28
1954	June	2	—	—	—	—	2	8	12
	July	9	7	—	—	—	7	7	30
	Aug.	2	38	5	—	—	8	2	55
	Sept.	1	8	1	1	—	—	—	11
1952–54	June	5	—	—	—	—	2	13	20
	July	21	19	2	—	—	13	10	65
	Aug.	16	108	9	3	—	15	4	155
	Sept.	4	48	13	3	1	—	—	69
	Total	46	175	24	6	1	30	27	309

* DGF = Developing Graafian follicle > 30 mm.

† RFCL = Recently formed corpus luteum.

Of 33 females from which ear plugs were collected, pairs of ovaries from 16 individuals were also collected. Table 5 shows the lengths and number of corpora albicantia present in the ovaries of these individuals.

As laminations are assumed to form at the rate of two per year after birth it would be expected that whales taken on the breeding ground would exhibit an even number of laminations in the core of the wax plug. However, such is not the case, and the difference may be due either to incorrect counting of the laminations or to the fact that the plugs examined were taken from whales over a protracted period during which time both northward and southward migrating whales would be sampled. Thus, the southward migrating whales would have accumulated an even number of fully formed laminations whilst the northward migrating whales would have accumulated an odd number of laminations.

TABLE 5

LENGTH AND CORPORA ALBICANTIA DATA ON 16 WHALES FROM WHICH CORES OF WAX EAR PLUGS WERE EXAMINED

Whale Length (ft)	No. of Laminations	Adjusted No. of Laminations	No. of Corpora Albicantia
42·92	18	16	8
41·00	14	12	2
42·25	15	14	8
45·50	25	24	6
48·25	34	32	20
44·83	21	20	6
44·17	20	18	5
42·33	19	18	10
40·75	13	12	6
42·83	18	16	6
43·58	18	16	14
41·67	15	14	8
41·82	14	12	3
45·25	25	24	19
47·00	27	26	6
42·58	17	16	12

Again by plotting corpora albicantia (i.e. total number of ovulations prior to the current ovulatory season) against total ear plug laminations to determine the rate of ovulation, an error of +1 year is introduced into the calculations when correlating the two variables, i.e. the correlation would show the current age with the total ovulations up to the previous ovulating season only.

In this paper it is proposed to adjust for the points mentioned by subtracting two laminations from the count in cores with an even number of laminations and one from the count in those with an odd number. In this way the laminations are corrected to the corresponding number of corpora albicantia.

Using the adjusted data (Table 5) the regression equation becomes $Y = 0\cdot 55x - 1\cdot 27$ (Y = corpora albicantia, x = laminations) which gives an ovulation rate of 1·10 corpora for every two laminations. In Figure 7 the standard error of estimates made from the line of best fit is about 6 per cent. If 95 per cent. confidence limits are placed on the data the slope could show a rate varying from 0·5 to 2 corpora for every two laminations. Using this method the average number of ovulations occurring in the puberal year is 1·10 and for this sample an average of 4·31 laminations has been formed at this stage (Fig. 7).

Another method used to determine the average rate of ovulation is that of fitting average rate curves to the data. Average rate curves for 2, 1, and 0·5 ovulations per two laminations are fitted commencing from each of the years at which puberty may be attained (Fig. 7).

This method, by taking into consideration both the varying rate of ovulation and the range of years at which puberty may be attained, gives a more satisfactory explanation of the data than the regression line around which there is a large scatter of values and on which little confidence can be placed.

By use of the fitted rate curves it is possible to derive an average rate of ovulation of 1·48 per year (Table 6) and an estimate of the possible age distribution at puberty, and in this sample the mean age is calculated to occur at 9·48 laminations (Table 6) (i.e. 4–5 years).

IV. Discussion

The outstanding problem in age determination in whales is that of discovering relationships between indices of age. The important indices used are those of growth periods in baleen, accumulated corpora albicantia, and laminations in the cores of wax ear plugs.

Of the three indices, laminations in the ear plugs of whales appear to offer the best method of age determination, especially if the assumption is true that two dark laminations are formed, corresponding to the northward and southward migration each year (Laws and Purves 1956). This assumption can be verified only by marking large numbers of suckling and yearling whales and studying the relevant data on ovaries, ear plugs, and baleen from these marked whales when they are recovered in later years.

Baleen plates may be used to determine age in young whales until wear at the tip has removed those characteristic sections of the plate which are recognizable as having been formed pre-natally and during the first year of life (i.e. suckling and weaning periods). The notation of 0+, 1+, etc. used for age groups is followed because, when reading baleen traces, full growth periods together with a portion of another growth period are seen. The amount of baleen which lies below the gumline is estimated to be equivalent to approximately 9 months' growth. Thus, the 0+ to 3+ age groups become 1 to 4 years old respectively. After this stage, owing to wear, the baleen loses its usefulness as an age determinant and for whales older than 4 years the notation 4+ etc. has to be applied.

It has been shown (Tables 3, 4, 5, and 6; Figs. 5, 6, and 7) that several different rates of ovulation may be calculated. For example, the observed number of ovulations for all mature whales examined from June to September was calculated to be 1·10–1·13. This estimate must be considered minimal because the calculation takes into consideration mature whales which had been killed prior to the first oestrous cycle and late pregnant whales which may have ovulated post partum, but does not consider killed whales which, unfertilized during the first oestrus, may have ovulated again later in the season.

The trend toward polyoestry is shown in Figures 5 and 6 and Mathews (1937) shows that the main mating season extends from July to November, but mating can take place throughout the year. Careful observation of the uteri of whales which had experienced one or two oestrous cycles during the 1954 season showed that of 60 whales only 13 (21·6 per cent.) possessed an early developing embryo. It is probable that in some cases embryos, lying between the endometrial folds, were unobserved, but the number overlooked is considered to be small, as embryos ranging

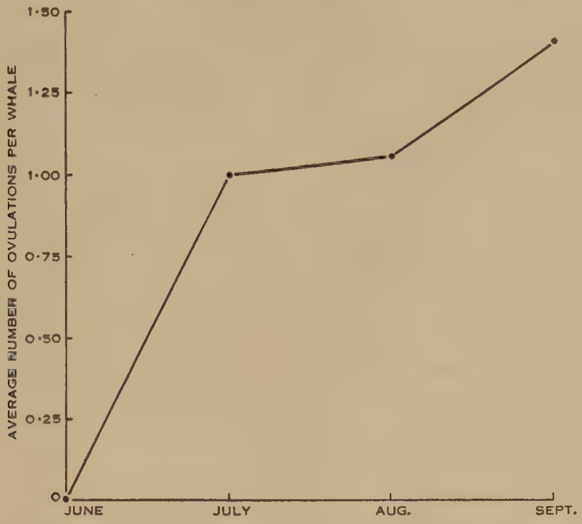

Fig. 5.—Seasonal increase in average number of ovulations per puberal whale.

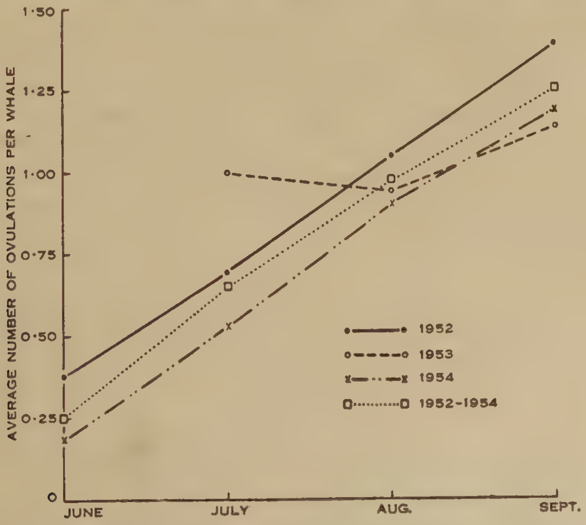

Fig. 6.—Seasonal increase in average number of ovulations per whale.

in size down to 0·1 in. were collected without trouble. Flushing of the Fallopian tube and isthmus failed to produce a blastocyst in those whales which had ovulated some time previously and whose uterus did not produce an embryo. It could be assumed that many of the whales unfertilized during the first oestrous period go into anoestrus until the next breeding season, in which case the ovulation rate would remain at about 1·13. However, evidence given by Symons and Weston

Table 6

CALCULATION OF AVERAGE RATE OF OVULATION AND YEARS AT WHICH PUBERTY MAY HAVE BEEN ATTAINED BY INDIVIDUALS SHOWN IN FIGURE 7

No. of Laminations	No. of Whales with an Average Ovulation Rate of			No. of Whales which may have Attained Puberty
	2/2 Laminations	1/2 Laminations	0·5/2 Laminations	
4	1	—	2	3
6	1	1	1	3
7	1	—	—	1
8	3	1	1	5
10	2	3	—	5
11	1	—	—	1
12	2	—	—	2
14	1	1	—	2
15	1	—	—	1
16	1	1	—	2
Total	14	7	4	25

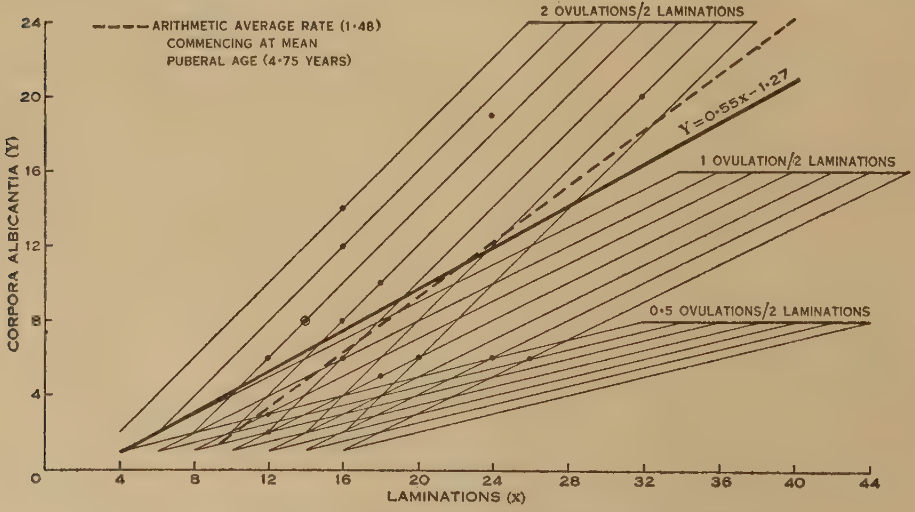

Fig. 7.—Relationship between corpora albicantia and laminations.

(1958) showed that, in the Antarctic, of the non-lactating sexually mature whales 82 per cent. were pregnant.

The discrepancy between the observed percentages of early pregnancies in tropical waters and late pregnancies in Antarctic waters could be explained by assuming that a much higher number of early pregnancies was overlooked in whales which had ovulated only once, or that those whales not fertilized during their first oestrous period ovulated again with successful fertilization later in the season.

The near coincidence of the observed rate (1·1–1·13) with the rate (1·10) calculated by the method of least squares can be considered fortuitous, for it was shown that little confidence could be placed in the regression of corpora albicantia on laminations. The poor correlation of corpora albicantia is most probably due to both the varying individual rates of ovulation and the age range over which puberty is attained.

The rate of ovulation (1·48) determined by fitting rate of ovulation curves, which take into consideration the varying rates of ovulation and the range of years over which puberty may be attained, affords a more satisfactory explanation of the data than the regression line around which there is a large scatter of values.

V. Acknowledgments

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A STUDY OF CONDITION (WEIGHT FOR LENGTH) OF AUSTRALIAN BARRACOUTA, *THYRSITES ATUN* (EUPHRASEN)

By M. Blackburn*

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Summary

Regression of weight in the round (w) on length to caudal fork (l) was calculated for 6571 barracouta from southbern Victoria and 2711 from south-eastern Tasmania. The equations for the regressions, which differ significantly in position but not in slope, are respectively $w = 0\cdot0572\, l^{2\cdot360588}$ and $w = 0\cdot1064\, l^{2\cdot238524}$. The values of the exponents are unusually low.

A condition factor K_n was obtained for each fish by dividing the observed weight by the weight estimated from the regression, and geometric mean K_n was calculated for each month for each of the two regions. The mean for southern Victorian fish varied within the year in much the same way in each of three successive years, with three highs and three lows from early spring through early winter, but was consistently higher in 1950–51 than at the corresponding period of the year in 1949–50 or 1951–52. A similar pattern of within-year variation is suggested by the scantier data for other years, and likewise for south-eastern Tasmanian fish. All changes in mean K_n are closely paralleled by those in mean $K_{n,c}$, the corresponding factor for beheaded eviscerated fish. It is also shown that changes in density of the fish are negligible. Thus the rises and falls in mean K_n represent true increments and decrements of growth in weight and volume of trunk muscle (edible flesh), unassociated with growth in length.

There is a tendency for fish with filling gonads to have better condition than ripe, spent, recovering, or immature individuals, but it does not explain the major part of the variation in condition observed. Neither is there any apparent relationship between mean K_n and percentage of the monthly sample affected by the sporozoan *Chloromyxum* or the cestode *Tetrarhynchus*, which cause the conditions known as "milky" and "wormy" and are the only parasites of barracouta that occur in the trunk musculature. It seems most likely that the changes in mean K_n signify a complex interplay between assimilation on the one hand and the energy demands of migratory and food-seeking activity on the other.

Oil content as a percentage of original (wet) weight was determined separately for fillet (edible flesh), viscera, and head of each of 66 south-eastern Tasmanian barracouta. There is a highly significant correlation between the oil content of each portion and the K_n of the fish. Regressions are given, and indicate that oil contents for fish of average condition ($K_n = 1\cdot000$) are 4·39, 8·08, and 7·98 per cent. for fillet, viscera, and head respectively.

I. Introduction

The gempylid scombriform fish *Thyrsites atun* (Euphrasen), a pelagic species, exhibits considerable variation in weight and fatness at similar lengths. This phenomenon is well known in the fisheries of South Africa, where *T. atun* is called "snoek"; observers distinguish "fat" and "poor" (thin) snoek, which tend to occur at different

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seasons (poor snoek in spring, fat snoek from summer to early winter) although they are sometimes found together (Gilchrist 1914; Hart 1946; Biden 1948; Davies 1954). In the Otago district of New Zealand, where *T. atun* are observed from October through July, they are very thin at the beginning of that period and in "best condition" at its end (Graham 1939).

There is no scientific literature on this subject for the Australian *T. atun* (barracouta) although fishermen are well aware of such variations; for instance exceedingly thin specimens are called "axe-handles" because the head is deeper than the trunk in side view. Plate 1(*a*) shows an Australian barracouta that is fatter than average; the pectoral region is much deeper than the posterior part of the head, the dorsal profile is convex for most of the distance between the pectoral and pelvic girdles, and the ventral profile also is convex. Plate 1(*b*) shows a fish that is thinner than average; the pectoral region is very little deeper than the posterior part of the head, the dorsal profile is practically straight between the two girdles, and the ventral profile is concave. These are by no means the extremes in bodily condition of Australian barracouta; neither the fattest fish nor the typical "axe-handle" is illustrated.

Data for a study of this subject were accumulated from the spring of 1948 through the autumn of 1955 in the course of a general investigation of the life history and availability of barracouta in southern Australian waters (see Blackburn and Gartner 1954; Blackburn 1957, for previous reports).

Copious data are available for barracouta of the southern coast of Victoria (areas IX, X, XI, XII of Blackburn and Gartner 1954; Blackburn 1957) and the south-eastern coast of Tasmania (areas I, II, III, Blackburn and Gartner 1954). The fish of these two regions belong respectively to two different populations, with the reservation that those occurring in area IX in June, July, and August represent part of a third population (Blackburn and Gartner 1954): the latter are not considered in this paper. The scanty data from the Furneaux Islands region in eastern Bass Strait (area V, Blackburn and Gartner 1954) have been utilized, for reasons given in Section IV(*d*) of this paper. The data from other regions were insufficient for analysis. All fish were caught at or near the surface of the sea with conventional barracouta fishing gear (troll lines and poles) except where otherwise stated.

Measurements of whole fish (l) were made to the nearest cm from the tip of the lower jaw (the most anterior part of the fish) to the fork of the caudal fin. This measurement was called "length to caudal fork" (L.C.F.) by Blackburn and Gartner (1954). Measurements of beheaded cleaned fish (l_c) were made to the nearest cm from the most anterior part of the carcass to the caudal fin fork. All fish were beheaded in the same way, namely that used by fishermen in areas VII and XIV (Blackburn and Gartner 1954).

Weights of whole fish (w) and beheaded cleaned fish (w_c) were recorded shortly after capture in g or oz (depending on the weighing scale available), as accurately as possible on the deck of the catching vessel at sea. Readings in oz were converted to g and all were rounded to the nearest 50 g, which appeared to be about the limit of accuracy under average sea conditions. Some readings had to be made to the nearest 100 g or the nearest 4 oz. The beheaded cleaned fish had head and all viscera, but not the backbone and tail, removed; almost the whole of the Australian commercial catch of barracouta is landed in this condition.

The noun "fatness" and adjective "fat" in this paper refer to the form of the fish and not to its oil content, which is discussed in Section V.

II. CALCULATION OF CONDITION FACTORS

"Condition" in fisheries biology generally signifies heaviness relative to expected average weight at any given length of fish, and is used here in that sense. The condition of a fish is described by a "condition factor", "coefficient of condition", or "ponderal index".

Le Cren (1951) has done much to eliminate misunderstandings about the calculation and use of condition factors. A brief summary of some of his remarks, together with additional observations which may help to make condition factors more meaningful to some workers, is given below.

A "condition factor" (K) and "relative condition factor" (K_n) may be distinguished. The former factor is based upon the hypothetical length–weight relationship from the cube law

$$w = cl^3, \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (1)$$

where w and l are weight and length respectively, and c is a constant. The latter factor is based upon the relationship

$$w = al^n, \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (2)$$

where w and l are as before, a is a constant equivalent to c, and n is a constant to be determined empirically.

Departures from these relationships for individual fish may be measured by the factors K and K_n in the equations

$$K = w/cl^3, \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots (3)$$

and

$$K_n = w/al^n, \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots (4)$$

in which c or a can be changed into a round number and then into its reciprocal, e.g.

$$K = 100w/l^3,$$

as by many authors, e.g. Hart (1946); and

$$K_n = 1{,}000{,}000w/l^{3\cdot 26},$$

as by Hart *et al.* (1940), who used the symbol C instead of K_n.

The procedure just mentioned is convenient with equation (3) since c is not known; but with equation (4), where a is found empirically at the same time as n by calculating the regression of w on l (Section III), it is preferable to work with the unaltered a. In equation (4) al^n is then equivalent to W, the weight estimated from the regression, and the equation becomes

$$K_n = w/W \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots (5)$$

That is to say K_n, the "relative condition factor" of Le Cren (1951), is the observed weight divided by the predicted weight for the observed length of the fish. Values of K_n fluctuate around $1\cdot0$, the differences from $1\cdot0$ representing the deviations from regression ($d_{w.l}$) as proportional parts of a standard $W = 1\cdot0$. For example, $K_n = 1\cdot043$ is equivalent to $(W+d_{w.l})/W$ where $W = 1\cdot000$ and $d_{w.l} = 0\cdot043$, so the weight of the fish is 4·3 per cent. above the average estimated from the regression of w on l.

These deviations of K_n from 1·0 describe all variations in w not associated with l, i.e. all that investigators generally have in mind when they attempt to study "condition" (genetic variation, and variation associated with food supply, sexual condition, parasitism, etc., including densimetric variation as noted below), in a way that is impossible with the other condition factor K unless n actually equals 3·0, which is rarely the case. If $n < 3\cdot0$, w in equation (3) will increase more slowly than l^3 and K will fall as l rises; if $n > 3\cdot0$, K will rise as l rises. Beverton and Holt (1957) stated that important departures from isometric growth ($n = 3\cdot0$) are rare. However, it is shown in Section III that n is considerably below 3·0, indeed lower than ever previously recorded, in each of the investigated barracouta populations, and it was noted that K did fall as l rose. The relative condition factor K_n is thus superior to the more frequently used condition factor K (Le Cren 1951) and was employed in this study. Sivertsen (1945) and Hart (1946) calculated K values for a few *Thyrsites atun* obtained in the South Atlantic.

A defect of both these condition factors is that differences between actual and expected weight may theoretically be differences between actual and expected volume, actual and expected density, or both. Differences in density could arise "from seasonal physiological changes or to permit of changes of habit" (Kesteven 1947). Kesteven proposed the use of two condition factors, one to measure departures from standard volume for a given length and one to measure departures from standard specific gravity, and suggested that volume be estimated from several measurements of each fish. Tester (1940) measured specific gravity of Pacific herring (*Clupea pallasii*) by immersion methods and showed that specific gravity divided by specific gravity minus one was a good index of "condition" of the kind in which he was interested, namely the oil content.

The conditions under which data on barracouta were gathered removed the possibility of using immersion methods or making several measurements of each fish. However, as shown in Section V, the estimated specific gravity of these fish ranges from 1·057 to 1·074, so that it varies by no more than 1·6 per cent.; but volume obviously varies much more, even in fish of the same length. The fish shown in Plate 1(*a*) had $K_n = 1\cdot101$, i.e. it was 10·1 per cent. heavier than the average for its length; and the specimen in Plate 1(*b*) had $K_n = 0\cdot866$ and so was 13·4 per cent. lighter than the average for its length. If the two fish had had the same length the fatter one would have weighed 27·1 per cent. more than the thinner. The increase in volume would have been much the same as this, whatever the specific gravities were: between 25·2 and 29·3 per cent., according to whether the thin and fat specimens had respectively the minimum and maximum specific gravities mentioned above, or vice versa. It is obvious from a comparison of the figures, bearing in mind that fish which show such differences in thickness dorsoventrally exhibit similar differences from side to side, that the percentage increase in volume is actually of this order, length for length. Densimetric variation may thus be ignored in interpreting large changes in K_n, and it is shown in Section V that almost all changes in K_n may be interpreted as involving parallel changes in volume of the fish.

For whole fish the principal condition factor employed was therefore $K_n = w/W$, where w = observed weight, $W = al^n$, l = observed length, and a and n were found from the regression of w on l. There were two regressions, one for Victorian and one for Tasmanian fish, each with its own a and n (Section III, Table 1). For beheaded cleaned fish the condition factor used was $K_{n,c} = w_c/W_c$, where w_c = observed weight, $W_c = al_c^n$, l_c = observed length, and a and n were found from the regression of w_c on l_c. There were two regressions, one for Victorian and one for Tasmanian fish (Section III, Table 1). Values of W and W_c were found by using the regression equations in logarithmic form. All means of K_n and $K_{n,c}$ mentioned in this paper are geometric means.

III. LENGTH–WEIGHT RELATIONSHIPS IN TWO POPULATIONS

As mentioned in Section I, southern Victorian and south-eastern Tasmanian data refer to two different biological populations of barracouta. The four regressions of weight on length mentioned in Section II, one for whole and one for beheaded cleaned fish of each population, are given in Table 1.

Plots of geometric means of weight against length on double log graph paper showed that the regression of log weight on log length was linear for all the data of each of the four sets. There was the expected scatter at the extremes of each range where numbers of observations were few, but nothing to indicate the existence of more than one stanza of relative growth in weight as mentioned for some species by Martin (1949). However, only 3·5 per cent. of the whole Victorian fish and only 0·4 per cent. of the whole Tasmanian fish measured less than 56 cm, the size at which sexually mature and immature fish occur in approximately equal numbers (Blackburn and Gartner 1954, Table 3), so there could be additional stanzas of growth in juvenile barracouta which the data of this investigation could not be expected to reveal.

Accordingly a single linear regression of log weight on log length was calculated for all the data of each of the four groups, using mean of log weight as the dependent variable y and log length as the independent variable x; as there was highly significant heterogeneity of variance of log weight in each group of data the x and y of each pair were multiplied by a weighting coefficient (ν times reciprocal of the variance of the ν values of y recorded for the given x). The final calculated regressions had the form

$$y = a' + nx,$$

where n measures the slope of the regression line and a' its position. The constants a' and n and their standard errors were calculated. Finally the equations were rewritten in terms of the original variables. The four equations in this form, together with the standard errors of a' and n, are given in Table 1.

Figure 1 shows the regressions for groups 1 and 2, i.e. Victorian and Tasmanian whole fish, in terms of w and l on logarithmic scales. There is no significant

TABLE 1

EQUATIONS FOR REGRESSIONS OF WEIGHT (w, w_c) ON LENGTH (l, l_c) OF BARRACOUTA

No.	Material	No. of Fish	Range of Lengths (cm)	Geometric Mean of Lengths (cm)	Equation ($w = al^n$)	$a' = \log a$	Standard Error of a'	Standard Error of n
1	Victoria (whole fish)	6571	31–111	72	$w = 0{\cdot}05720\ l^{2\cdot360588}$	−1·2426	0·0273	0·041201
2	Tasmania (whole fish)	2711	37–112	79	$w = 0{\cdot}1064\ l^{2\cdot238524}$	−0·9732	0·0465	0·075864
3	Victoria (beheaded cleaned fish)	4257	25–87	56	$w_c = 0{\cdot}08630\ l_c^{2\cdot305839}$	−1·0640	0·0386	0·033520
4	Tasmania (beheaded cleaned fish)	1878	29–93	63	$w_c = 0{\cdot}3986\ l_c^{1\cdot957300}$	−0·3995	0·0763	0·061020

difference between them as regards slope n but there is a highly significant difference as regards position a'. This supports the observation of Martin (1949) that lines describing length–weight relationships in different populations of a fish species tend to run parallel, but it does not constitute strong additional evidence of population difference. Regressions 3 and 4 are significantly different in both slope and position, but refer to mutilated specimens.

Blackburn and Gartner (1954) gave an equation for estimating l from l_c for Victorian and Tasmanian barracouta, namely

$$l = 5 \cdot 329 + 1 \cdot 165\, l_c.$$

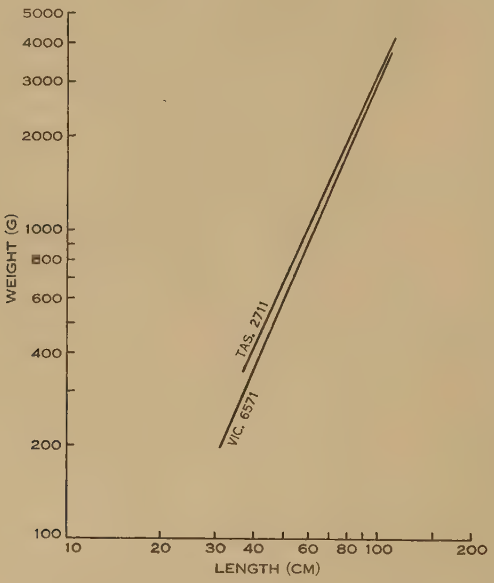

Fig. 1.—Regressions of weight (w) on length (l), on logarithmic scales, for southern Victorian and south-eastern Tasmanian barracouta (whole fish); see Table 1, equations 1 and 2.

The longest and heaviest barracouta recorded in this investigation in southern Victorian waters measured 111 cm (to the caudal fork) and weighed 5000 g (11 lb). The longest and heaviest recorded in south-eastern Tasmanian waters measured 112 cm and weighed 5850 g (12 lb 14 oz). A specimen from another part of the Australian coast (Lakes Entrance, eastern Victoria) was even longer (116 cm) although not heavier (4850 g). A Tasmanian specimen weighing 17 lb has been verbally reported. The greatest weight recorded in South Africa is 18½ lb (Biden 1948).

The value of the exponent n for whole barracouta, approximately 2·3, is probably the lowest on record for a length–weight relationship of unmutilated fish. The author knows of no values below 2·5 or over 4·0, the range mentioned by Le Cren (1951).

IV. Time Changes in Mean Condition Factors in the Same Population

(*a*) *Variations within the Year*

Most of the observations in this and other subsections of Section IV refer to southern Victorian fish, which all belong to the same biological population. Specimens taken in area IX in June, July, and August were disregarded, for reasons given in Section I. The bulk of the material was obtained between Westernport and Apollo Bays, along about 100 miles of coastline.

Table 2 gives, for southern Victorian fish: (1) the mean K_n for each month in which data for ten or more fish were available, and the number of fish; and (2) the mean $K_{n,c}$ for each month similarly, and the number of fish. The $K_{n,c}$ usually were calculated from only part of the K_n monthly sample, which was frequently a composite of several samples from different localities.

Figure 2 shows these means plotted against time. The squares refer to observations on Furneaux Islands fish which are discussed in Section IV(*d*). Some of the points have been connected by lines to show trends in condition more clearly, but others have not been so connected because of uncertainty about the trends, a matter which is discussed in Section IV(*d*). This subsection deals with variations in mean K_n within the year; variations between years are discussed in Section IV(*b*).

The succession of changes in mean K_n within the period of availability of barracouta, which is normally from September to May, June, or July, appears to be rather similar in each of the years 1949–50, 1950–51, and 1951–52. Peaks and troughs, the latter indicated by arrows in Figure 2, occur in an order that may conveniently be summarized as follows:

1. a "spring high" in September and October, which may last through December, noted in each of the three years;
2. a "summer low" which may occur from November to January, noted in each year;
3. a "summer high", reaching a maximum from January to March, noted in each year;
4. an "autumn low" which may occur from January to May, noted in each year;
5. an "autumn high" which may occur from April to June, noted in each year;
6. a "winter low" in June or July, noted in two of the three years (no observations were made in the winter of 1951–52).

The fragmentary series of monthly means of K_n available for smaller samples in three other years appear to conform to this pattern as far as they go (Table 2, Fig. 2). In the 1948–49 series the spring high, summer low, and summer high may be identified; in 1952–53 the summer low, summer high, and autumn low are evident, and the mean for July 1953 may indicate the winter low; in 1953–54 there are signs of most stages from summer low (as early as late October, see below) through winter low (June).

TABLE 2

GEOMETRIC MEANS OF VARIOUS CONDITION FACTORS (K_n AND $K_{n,c}$) IN MONTHLY SAMPLES OF BARRACOUTA FROM AREAS IX TO XII, WITH NUMBERS OF OBSERVATIONS CONTRIBUTING TO EACH MEAN

Period	K_n	No.	$K_{n,c}$	No.
Nov. 1948	0·931	140	0·889	50
Jan. 1949	0·842	17	0·792	17
Feb. 1949	0·952	285	0·933	267
Mar. 1949	0·950	45	0·908	44
Sept. 1949	1·091	80	1·006	53
Oct. 1949	1·028	26	0·962	26
Dec. 1949	0·850	179	0·797	175
Jan. 1950	0·932	201	0·908	136
Feb. 1950	0·943	233	0·914	39
Mar. 1950	1·015	154	1·049	99
Apr. 1950	1·002	282	1·038	175
May 1950	0·980	394	1·050	140
June 1950	1·025	699	1·136	213
July 1950	0·680	116	0·625	104
Sept. 1950	1·235	56	1·307	48
Oct. 1950	1·239	139	1·364	111
Nov. 1950	1·043	156	1·019	140
Dec. 1950	1·247	314	1·058	126
Jan. 1951	1·240	266	1·376	165
Feb. 1951	1·129	21	1·283	21
Mar. 1951	1·190	56	1·334	52
Apr. 1951	1·286	100	1·468	99
June 1951	0·901	108	0·940	69
Sept. 1951	0·991	136	1·012	49
Oct. 1951	1·299	21	1·448	21
Nov. 1951	1·023	64	1·039	64
Dec. 1951	1·028	100	0·963	50
Jan. 1952	0·825	171	0·895	50
Feb. 1952	1·015	150	0·797	54
Mar. 1952	0·664	106	0·610	53
Apr. 1952	0·884	90	0·940	30
May 1952	0·841	37	0·866	37
Nov. 1952	0·920	62	0·941	61
Feb. 1953	0·937	25	0·916	25
Mar. 1953	1·079	178	1·018	59
Apr. 1953	1·024	37	0·892	17
July 1953	0·862	41	1·027	41
Oct. 1953	0·826	50	0·831	75
Nov. 1953	—	—	0·990	100
Dec. 1953	0·939	101	0·929	96
Jan. 1954	1·040	50	1·019	50
Feb. 1954	1·026	150	1·068	149
Mar. 1954	1·034	46	1·065	44
Apr. 1954	1·023	26	1·005	26
June 1954	0·897	202	0·939	201

There may be an additional stage, a "spring low" preceding the spring high, but it seems improbable that it occurs regularly, if at all. It is suggested only by the data for 1951–52 and 1953–54. The K_n means for the five months September 1951 through January 1952 are respectively 0·991, 1·299, 1·023, 1·028, and 0·825, which could indicate a spring low in September, spring high in October, and summer low developing from November to January. However, the October mean is suspect because it is based on only 21 fish, and it could reasonably be concluded that there was a spring high from September through December with mean K_n generally about 1·0, followed by a summer low in January. The data for the early part of the 1953–54 season could be interpreted as spring low in October, spring high in November, summer low in December, and summer high in January: but the November mean actually is for $K_{n,c}$, not K_n (Fig. 2), and if it is ignored the October mean can readily be interpreted as the summer low, occurring earlier than in any of the other years; actually the October mean is based on material taken very late in that month, and the summer low can occur in November, so the second interpretation is quite reasonable.

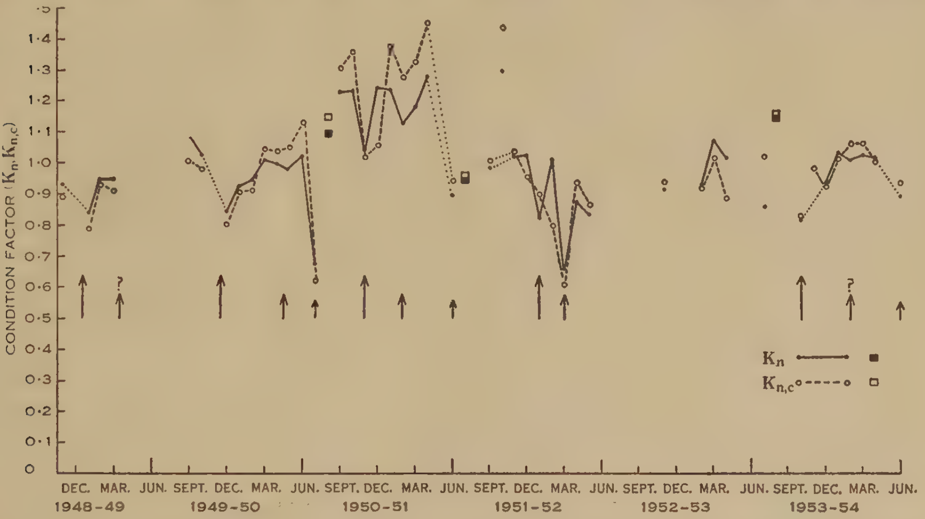

Fig. 2.—Changes in geometric mean of various condition factors (K_n and $K_{n,c}$) for southern Victorian barracouta (see Table 2 for data); with additional points plotted as squares for Furneaux Islands fish (see Section IV(d) for data). Arrows indicate lows of condition discussed in Section IV(a). Dotted lines represent interpolations.

For each year except 1951–52 the three highs are comparable as regards level of K_n, but the three lows are not; the summer low is lower than the autumn low and the winter low is lower still. The situation in 1951–52 is quite different (Fig. 2): however, the apparent peak of the spring high in October is suspect, as indicated above, and the lowness of the autumn low and autumn high is probably due in part to peculiarities in the size-composition and gonad-stage-composition of the part of the population available at that period, which are discussed in Section IV(c).

Figure 2 shows that trends in mean $K_{n,c}$ are very similar to those in mean K_n, much more so than might have been expected in view of the generally smaller numbers of observations on $K_{n,c}$. The only important discrepancies are in December 1950, February 1952, and July 1953, the first two of which could be explained by the smaller numbers of observations on $K_{n,c}$, although the third could not (Table 2). It can definitely be stated that seasonal (and annual) changes in condition of the whole fish are closely matched by changes in condition of the eviscerated trunk, i.e. the edible portion; that is to say, the changes in the whole fish are not primarily the result of changes in weight of head, gonads, other viscera, or stomach contents.

TABLE 3

GEOMETRIC MEANS OF CONDITION FACTORS (K_n AND $K_{n,c}$) IN MONTHLY SAMPLES OF BARRACOUTA FROM AREAS I TO III, WITH NUMBERS OF OBSERVATIONS CONTRIBUTING TO EACH MEAN

Period	K_n	No.	$K_{n,c}$	No.
Jan. 1949	0·884	105	0·902	100
Apr. 1949	1·064	11	1·074	12
May 1949	1·030	263	1·074	160
Dec. 1949	0·942	100	1·019	48
Mar. 1950	0·994	432	1·080	216
Aug. 1950	1·091	23	1·114	22
Nov. 1950	1·126	114	1·206	98
Mar. 1951	1·095	47	1·187	47
Apr. 1951	0·829	81	0·843	78
May 1951	0·904	115	0·918	115
Nov. 1951	0·874	34	0·937	34
Dec. 1951	0·861	199	0·906	100
Feb. 1952	1·153	187	1·215	49
Mar. 1952	0·956	132	1·004	100
Apr. 1952	1·045	47	—	—
Dec. 1952	1·064	194	1·038	149
Feb. 1953	0·958	151	0·973	102
Apr. 1953	0·951	153	0·894	152
June 1953	0·913	83	0·853	83
Jan. 1955	0·965	122	0·942	100
Mar. 1955	0·916	20	0·921	20
May 1955	0·939	10	1·047	10

Although most of the highs and lows of K_n are represented by means (geometric) based on large numbers of observations, it was felt to be desirable to obtain some indication of the 95 per cent. confidence limits of the means. Limits were found for ten means by calculating mean ± ($t_{0\cdot05}$ × standard error) for log K_n, and transforming.

The ten means were those for December 1949; February, March, November, December 1951; January, February, April, May 1952; and October 1953: numbers of observations ranged from 21 to 179 (Table 2). The widest confidence interval was for the sample of 50 for October 1953, which was +0·065, −0·060; the narrowest was for the sample of 150 for February 1952, which was +0·014, −0·015; the widest for a sample of 100 or more was +0·024, −0·023 (January 1952).

It may be concluded that the lower limits of significant difference between K_n means are about 0·09 if one mean is based on 100–200 observations, about 0·05 if both means are so based, and lower if the numbers of observations exceed 200. On this basis there is virtually no doubt about the significance of any of the high–low differences mentioned above, and shown in Figure 2 and Table 2, except those between March and April 1953 (shown better by $K_{n,c}$ than K_n data; probably significant) and those between January and April 1954.

Similar but more scattered data are available for south-eastern Tasmanian barracouta, which belong to a different population (Table 3). The season of availability in this region is shorter, from November to May or June.

Within each such season, it will be noted from Table 3, there is much variation in mean K_n and $K_{n,c}$, broadly between 0·8 and 1·2 as in southern Victoria. There are insufficient observations for successive months to indicate any general pattern of variation in condition within the year, but there could be a pattern similar to that demonstrated for southern Victorian fish. The series of means for the period November 1951 through April 1952, for which only January data are lacking, shows a low in November and December, a high in February, a low (not as marked as the previous one) in March, and recovery in April; these could be identified with the summer low, summer high, autumn low, and autumn high of southern Victorian fish. The mean of April 1951, which is low compared with those of March and May of the same year, could also represent the autumn low. Similarly the isolated means for November 1950 and December 1952 could represent the spring high, and that for June 1953 the winter low. The only observation for any month from July through October is for August 1950, when K_n and $K_{n,c}$ were high; this is further discussed in Section IV(*d*). A positive correlation between mean K_n and mean $K_{n,c}$ is observable in these Tasmanian data, as it was in those for southern Victoria.

(*b*) *Variations between Years*

The fluctuations in mean K_n and $K_{n,c}$ within a single fishing season, described above, occur around a mean level which may change from year to year within the same population. Evidence of this is presented in Figure 2 for southern Victorian fish, whose condition was better at any particular high or low during 1950–51 than at the corresponding stage in any other season. The very high level of condition indicated at the beginning of 1951–52 is suspect, as noted in Section IV(*a*), and the low level at the end of that season, which is discussed in the following section, is partly due to an atypical distribution of size and gonad stage in the population. Only minor variation in average condition for the whole fishing season is indicated for the other four years.

The scantier data for south-east Tasmanian barracouta (Table 3) show nothing so obvious and justify no statement about variation in condition between years.

Two of the three highest monthly means of K_n were recorded in 1950–51 (November, March), but the lowest mean was also recorded in that year (April), and the highest mean of all was noted in February 1952.

(c) *Analysis of Variations by Sexes and Gonad Stages*

The monthly condition factor data on southern Victorian fish for 1949–50, 1950–51, and 1951–52 (Fig. 2) were analysed further, according to sex and gonad stage of the fish. Gonad stages were those listed by Blackburn and Gartner (1954), in brief: stage 1, immature and inactive, virginal; stage 2, immature but developing or recovering; stages 3 and 4, gradually filling; stage 5, full; stage 6, gametes shed readily, so rarely observed in females that it was included with stage 7 for that sex; and stage 7, spent. Stage 1 is characteristic of the smaller (<56 cm), stages 2 to 7 of the larger fish.

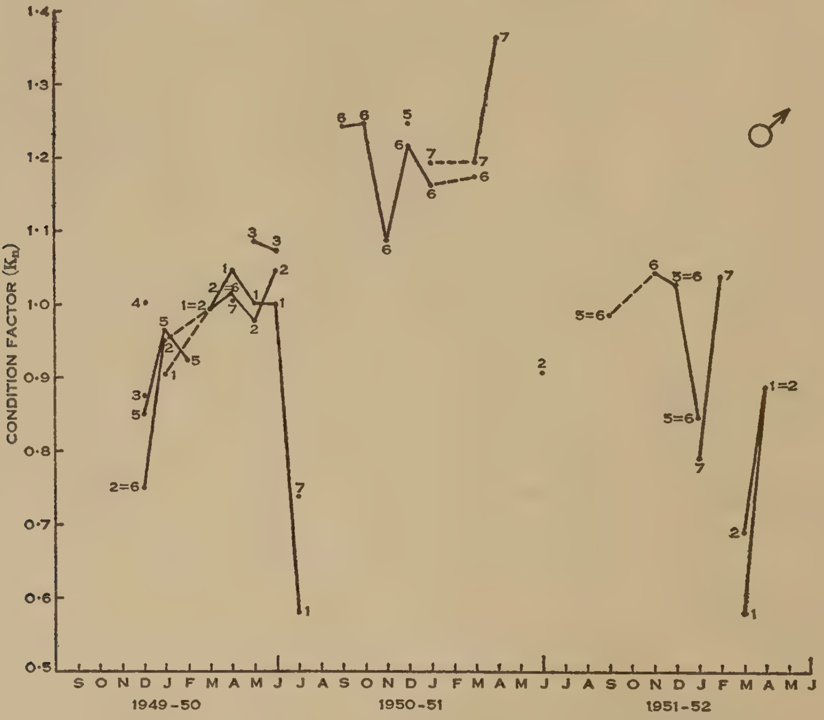

Fig. 3.—Changes in geometric mean of K_n for southern Victorian barracouta, male, with gonad stages as indicated by the numbers 1–7 and explained in Section IV(c). Dashed lines represent interpolations.

Figure 3 shows the geometric mean of K_n for males at each gonad stage for each month in which the stage was represented by ten or more specimens, and Figure 4 gives similar data for females. Figures 3 and 4 may be compared with Figure 2; the variations in Figure 2 discussed in Sections IV(a) and IV(b) cannot be followed quite as clearly in Figure 3 or Figure 4 because of the smaller amounts of data available and the manner in which they are presented, but many of the same features are observable. For instance the 1950–51 series of K_n means in Figure 3 is quite comparable with the same series in Figure 2, and the 1949–50 series in Figure 4 with that of the same year in Figure 2. The $K_{n,c}$ data were not analysed in this manner because they were less copious than those for K_n; but since monthly mean K_n and $K_{n,c}$ are so closely correlated it may be assumed that conclusions drawn below about K_n apply also to $K_{n,c}$.

Three points of interest in Figures 3 and 4 warrant special discussion. The first is that K_n means for fish of the same month, year, and gonad stage are generally almost the same for both sexes, and there is no clear indication that K_n is

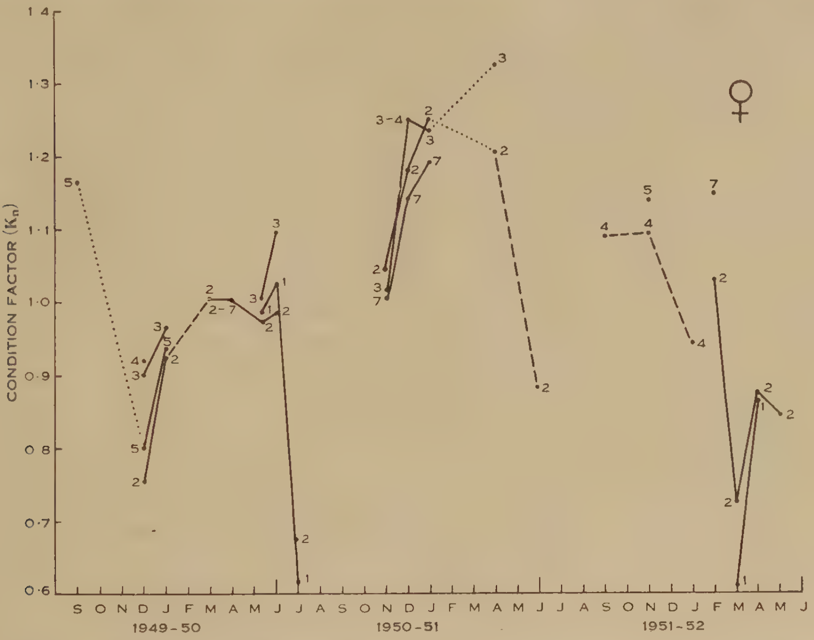

Fig. 4.—Changes in geometric mean of K_n for southern Victorian barracouta, female, with gonad stages as indicated by the numbers 1–7 and explained in Section IV(c). Dashed and dotted lines represent interpolations.

generally superior in one sex. For instance, comparisons can be made for 1949–50 between males and females at stages 1, 2, 3, and 5 in two or more months and at stages 4 and 7 in one month only; and similar comparisons can be made for material of the other two years, 24 comparisons in all between K_n for male and female at the same gonad stage in the same month over the three years. The differences in mean K_n in the 15 comparisons in which the male K_n was higher ranged from 0·005 to 0·085 (median 0·026) and those in the nine comparisons in which the female K_n was higher ranged from 0·007 to 0·031 (median 0·021). Possibly the average condition of males is slightly superior to that of females with gonads at the same stage in the same month, but it must be pointed out that the gonad stages overlap and that different observers recorded doubtful cases in different ways; and it seems safe to conclude that the sex of the fish is unimportant as a factor contributing to variation in K_n.

The second point of interest is that fish with gonads at certain stages tend to have higher K_n means than other fish, in any month in which the different stages are well represented. There are exceptions, which may be due to the abovementioned difficulty of recording gonad stages.

In Figure 3, for example, it can be seen that K_n for stage 4 was higher than K_n for stages 2, 3, 5, and 6, in the only month in which it occurred; that K_n stage 3 was higher than K_n for any stage except 4; that K_n stage 5 was higher than or equal to K_n stage 6, which was either a little higher or a little lower than K_n stage 7 and equal to K_n stage 2; and that K_n stage 2 differed little from K_n stage 1 in any month in which both occurred, except in March 1952 when K_n stage 1 was markedly the lower. The relationships between the mean K_n for the different male gonad stages may therefore be summarized:

$$1 \leqslant 2 < 3 < 4 > 5 \geqslant 6 \doteqdot 7 \doteqdot 2 \geqslant 1 \quad (3>5),$$

where each number stands for mean K_n at that gonad stage and the means are considered to be independent of month or year. This means that males with filling testes (stages 3 and 4) are in better average condition than those with full but not completely ripened testes (stage 5), and better still than those that are ripe, spent, recovering, or virgin (stages 6, 7, 2, and 1).

Figure 4 shows the same situation, less clearly, for females. Where stages 3, 4, and 5 or any two of them occur in the same month sometimes one stage has the highest (or higher) K_n, and sometimes one of the others. Stage 6, as explained above, is not represented. Mean K_n stage 2 can be approximately equal to or greater than K_n stage 1, and approximately equal to or less than K_n stage 3. Mean K_n stage 7 is less than K_n stages 3 and 4, and therefore probably less than K_n stage 5; and it may be equal to or greater or less than K_n stage 2. The relationships may be summarized in much the same way as for males:

$$1 \leqslant 2 \leqslant 3 \doteqdot 4 \doteqdot 5 > 7 \doteqdot 2 \geqslant 1,$$

which indicates better condition for filling or full fish than for those which are spent, recovering, or virgin.

The third point of interest is that these relationships do not account for all variation in mean K_n throughout the year; in fact most of the within-year variation whose pattern was described in Section IV(a) appears to be independent of gonad stage, as shown by the fact that the curves of mean K_n for different gonad stages tend to show the same succession of highs and lows as does the curve for all stages combined (Fig. 2). Naturally the entire succession of highs and lows is not shown by the K_n data for any single gonad stage, since no single stage would be expected to persist in abundance throughout the whole season of availability of the fish (Blackburn and Gartner 1954); but there is ample evidence of a similarity of succession in fish of gonad stages which are contemporaneous. Specifically, there is evidence in Figures 3 and 4 of the following changes in K_n for the following gonad stages, in one or more years:

Descent from spring high to summer low: ♂5, ♂6, ♀4, ♀5.

Ascent from summer low to summer high: ♂1, ♂2, ♂5, ♂6, ♂7, ♀2, ♀3, ♀5, ♀7.

Descent from summer high to autumn low: ♂1, ♂2, ♂6, ♀2.

Ascent from autumn low to autumn high: ♂1, ♂2, ♂7, ♀1, ♀2, ♀3.

Descent from autumn high to winter low: ♂1, ♀1, ♀2.

It is clear from these results that the succession of changes in average condition throughout the year is not merely, or even mainly, the result of the replacement of certain gonad stages by others where each stage is associated with a particular level of condition of the fish. There is replacement of stages, and some stages occur in better-conditioned fish than in others which are present in the same month, but there is no month-to-month uniformity of level of condition of fish with gonads at any particular stage. On the contrary, the curves of mean K_n for fish of different stages rise and fall together, in the way described in Section IV(*a*), and mean K_n is much more variable for fish of the same stage in different months than for fish of different stages in the same month.

Not only the within-year but also the between-year variations in mean K_n are paralleled by variations in mean K_n for fish of single gonad stages. The high general level of K_n in 1950–51, mentioned in Section IV(*b*), is evident not only for all fish combined but also for stage 6 and 7 males (Fig. 3) and stage 2, 3, and 7 females (Fig. 4). Similarly the low level of K_n in the autumn of 1952, mentioned in Section IV(*a*), is just as evident for each of the best-represented stages, namely stage 1 and 2 males (Fig. 3) and stage 1 and 2 females (Fig. 4), as for the combined material (Fig. 2). It may be noted that the autumn low and autumn high levels of K_n as shown in Figure 2 would probably have been higher but for an unusual scarcity of fish at stages other than 1 and 2 at the end of the 1951–52 season. It so happened that the adult members of the population were virtually absent from the coast in that autumn, leaving only juveniles of average length 55 to 60 cm, few of which could have developed beyond stage 2, available for capture (Blackburn and Gartner 1954).

The data for south-eastern Tasmanian fish are inadequate for analysis of variations by sex and gonad stage.

(*d*) *Condition in Winter*

As indicated in Section IV(*a*) and elsewhere (Blackburn and Gartner 1954), the winter, from June through August, is the season of greatest scarcity of barracouta of the principal population of the southern coast of Victoria. Normally fish are available but not abundant in June, scarce in July, and very scarce in August; they become available again in September and are reasonably abundant in October. The available data on mean K_n for winter fish are therefore rather sparse. So far, in this paper, attention has been drawn to the appearance of a winter low of condition in June or July, after which the record of mean K_n is broken until September, when the spring high is observed (Section IV(*a*), Table 2, Fig. 2).

Blackburn and Gartner (1954) gave reasons for believing that the barracouta which occur on the southern Victorian coast in spring, summer, and autumn migrate south-east to the Furneaux Islands region of eastern Bass Strait (area V, loc. cit.) in winter. Squares are plotted in Figure 2 to indicate mean K_n and $K_{n,c}$ for the monthly samples available from that little-fished region at that season, using W and W_c values as for Victorian fish. There are only three such samples, all from the eastern side of the Furneaux Group: for August 1950, off Babel Island, 46 fish for K_n (45 for $K_{n,c}$); July 1951, off Cape Barren Island, 20 for K_n (17 for $K_{n,c}$); and August 1953, off Babel Island, 6 for K_n and $K_{n,c}$ (trawled; see Blackburn and Gartner 1954, p. 459).

It will be seen from Figure 2 that the K_n means for August 1950 and July 1951 fall between the southern Victorian means for the winter low (July 1950, June 1951) and spring high (September 1950 and 1951), as might be expected if all the samples were drawn from the same biological population. The same might have been true of the mean for August 1953, but it is based on only six specimens and the level of the spring high for that year is not known. It seems probable that the recovery in level of K_n, from winter low at the end of the season of availability on the Victorian coast (June or July) to spring high at the beginning of the following season (September), takes place in the Furneaux Islands region.

The only record of mean K_n of south-east Tasmanian barracouta in any winter month is that for August 1950, which is 1·091 (Table 3). The condition of the members of this population can therefore be fairly high in late winter; this strengthens the possibility, mentioned in Section IV(*a*), that the annual cycle of fluctuations in condition is much the same for south-east Tasmanian as for southern Victorian fish.

V. OIL CONTENT AND CONDITION FACTOR

Several authors have investigated the relationship between some condition factor (frequently K, see Section II) and oil content of the fish, in different species. Hart *et al.* (1940) obtained a significant positive correlation between the two in Pacific herring, *Clupea pallasii*, and referred to similar investigations by various workers on the Atlantic herring, *C. harengus*. Others who observed a close positive relationship included Clark (1928) for the Pacific North American pilchard, *Sardinops caerulea*, and Davies (1956) for the South African pilchard, *S. ocellata*.

Rapson *et al.* (1944) and Van Wyk (1944) determined oil contents of livers, heads, intestines, and edible portions of South African *Thyrsites atun* at different times of year. Their results show a pattern of seasonal change (oil content maxima in autumn, minima in spring) which corresponds to that of the gross condition of the fish as mentioned in Section I of this paper. The only published oil content determinations for Australian barracouta are those of Jowett and Davies (1938) for various parts of seven specimens from south-east Tasmania. It is now possible to record further determinations for 66 south-east Tasmanian fish (areas I, II, and

III) which were obtained from November 1952 through February 1956 and processed in the Division of Food Preservation and Transport, C.S.I.R.O.

These results are given in Table 4. Each fish was measured and weighed in the round so that K_n could be determined. It was then divided into three portions, fillet (i.e. edible flesh), viscera (alimentary canal with contents, liver, pyloric caeca, heart, gonads, kidney, and associated structures), and head; the remainder of the fish, mostly backbone and tail, was not used. Each portion (about 250 g in the case of the fillet) was macerated into a paste from which a sample was taken for determination of oil content. This sample was triturated with anhydrous sodium sulphate and the powder Soxhlet-extracted with dry diethyl ether. Oil content was expressed as a percentage of the original (wet) weight of the portion of the fish.

The coefficients of correlation between K_n and oil content of fillet, viscera, and head are respectively 0·640, 0·607, and 0·536, each of which is significant at the 1 per cent. level of probability for the 64 degrees of freedom available for testing. As indicated in Section IV(*a*), too little is known about the pattern of change in mean K_n within the year in south-eastern Tasmanian fish to enable this correlation to be used to indicate the way in which oil content would vary with time. However, it may be concluded that the oil contents rise and fall with the highs and lows in mean K_n for south-eastern Tasmanian barracouta, whenever they occur; and probably also for southern Victorian barracouta, in view of the relationship demonstrated for the species in south-east Tasmania and South Africa.

Regression equations for estimating percentage oil content of fillet, viscera, and head from K_n, based on the data of Table 4, are as follows:

$$\text{Percentage of oil in fillet} = 13{\cdot}904\ K_n - 9{\cdot}510;$$

$$\text{Percentage of oil in viscera} = 25{\cdot}245\ K_n - 17{\cdot}167;$$

$$\text{Percentage of oil in head} = 14{\cdot}320\ K_n - 6{\cdot}339.$$

It follows that the best available estimates of oil content of fillet, viscera, and head of south-east Tasmanian barracouta in average condition ($K_n = 1{\cdot}000$) are 4·39, 8·08, and 7·98. These figures give some indication of the percentage of the total weight of the catch over a long period (at least one entire fishing season) that would be available as oil, for the three portions separately (see Section VII). The corresponding percentages for southern Victorian fish, which tend to be smaller and to have a less varied diet (Blackburn and Gartner 1954; Blackburn 1957), might be different, and a series of oil determinations for those fish would be of value.

The oil content of the fillet and head appears to be higher in South African than in south-east Tasmanian fish at similar stages of the annual condition cycle. For example the highest monthly K_n mean recorded for Tasmanian material is 1·153 (Table 3), from which the mean percentage of oil content in that month may be estimated, from equations above, as 6·5 for fillet and 10·2 for head; the highest monthly mean percentages recorded for South African fish are 9·5 for fillet and 19·5 for head (Rapson *et al.* 1944; Van Wyk 1944). The difference may be due to the fact that South African barracouta (snoek) feed to a much greater extent on oily fish than do those in Tasmania (Blackburn 1957); their average length is also greater.

TABLE 4

LENGTH (l), WEIGHT (w), CONDITION FACTOR (K_n), AND OIL CONTENT OF FILLET, VISCERA, AND HEAD AS PERCENTAGE OF WET WEIGHT FOR 66 SOUTH-EAST TASMANIAN BARRACOUTA CAUGHT AT THE DATES AND AREAS SPECIFIED

No.	Date	Area	l (cm)	w (g)	K_n	Oil Content (%)		
						Fillet	Viscera	Head
1	21. xi.52	III	84	2325	1·076	2·96	11·90	5·57
2			85	2466	1·112	3·62	6·80	4·18
3			90	2381	0·945	2·32	6·80	3·21
4			78	1871	1·022	1·96	3·14	4·40
5			82	2041	0·998	3·58	5·68	5·50
6			82	2268	1·108	7·46	8·26	10·04
7	9.xii.52	II	84	2523	1·168	5·57	6·87	8·58
8			88	2523	1·053	8·74	7·81	12·42
9			90	2693	1·068	7·02	8·34	12·37
10			85	2410	1·086	5·42	13·06	10·80
11			85	2268	1·022	6·94	7·60	10·07
12			81	2410	1·210	4·24	7·27	7·44
13	12. i.53	II	86	2126	0·934	1·01	4·18	3·82
14			69	1247	0·897	3·52	9·03	8·82
15			67	1162	0·893	3·14	6·92	9·58
16			81	1673	0·840	1·55	2·93	3·02
17			92	2495	0·942	2·41	3·27	4·48
18	24. i.53	III	89	2296	0·934	4·77	4·78	7·54
19	—. ii.53	II, III	80	1814	0·937	2·32	3·44	3·30
20			90	2013	0·798	1·25	1·98	4·00
21			82	1644	0·804	1·14	2·86	1·88
22			85	2296	1·035	5·22	12·30	9·73
23			81	2155	1·082	5·26	8·00	9·91
24			78	1786	0·976	2·38	3·53	8·11
25	15. iv.53	II, III	74	1984	1·220	5·56	12·62	11·38
26			83	1814	0·863	0·79	2·29	1·53
27			84	2041	0·945	2·10	6·03	7·36
28			99	2637	0·845	1·18	2·80	3·38
29			88	2353	0·982	1·12	3·72	4·66
30			65	1191	0·978	1·68	7·79	8·56
31	19. v.53	II, III	84	1673	0·774	1·01	2·62	2·55
32			92	2495	0·942	4·09	6·64	8·78
33			90	2155	0·855	1·74	4·00	3·76
34			82	1729	0·845	1·50	2·55	5·45
35			89	1984	0·807	1·77	4·72	7·90
36			94	2523	0·908	1·24	3·91	5·89

TABLE 4 (*Continued*)

No.	Date	Area	l (cm)	w (g)	K_n	Oil Content (%)		
						Fillet	Viscera	Head
37	—. iii.54	III	73	1446	0·916	2·98	3·92	10·56
38			61	964	0·914	3·07	6·54	8·80
39			56	737	0·845	4·99	10·56	9·43
40			53	567	0·736	1·33	3·70	7·18
41			49	454	0·702	0·72	2·33	4·70
42	29. iii.54	I	92	2268	0·856	3·16	3·69	5·12
43			86	2381	1·046	7·55	20·12	11·00
44			71	1503	1·013	7·22	10·76	9·48
45	27. iv.54	I	101	3969	1·216	11·12	31·14	13·00
46			87	2835	1·214	8·29	16·77	11·06
47			92	2552	0·963	2·23	3·80	7·52
48			91	2693	1·043	6·80	11·66	10·16
49			93	2693	0·993	8·05	12·41	13·52
50			102	3147	0·943	4·30	7·54	7·10
51	27. v.54	I	87	2126	0·910	4·44	9·70	9·38
52			88	2608	1·088	7·24	12·57	14·74
53			85	2552	1·150	6·29	17·30	11·20
54			84	2381	1·024	4·99	9·68	10·82
55			84	2381	0·919	6·85	13·94	11·78
56			89	2523	1·164	10·84	16·96	14·32
57	22.xii.55	I	103	3175	0·931	2·95	5·40	5·13
58			85	2353	1·061	2·60	3·36	3·28
59			95	3005	1·056	2·88	5·88	5·17
60			95	3005	1·056	3·17	5·25	3·96
61			84	2240	1·037	2·71	4·05	5·00
62			92	2722	1·027	3·27	6·44	8·45
63	4. ii.56	I	95	3289	1·156	7·08	6·92	10·17
64			92	2807	1·060	4·51	10·68	8·60
65			87	2778	1·189	6·92	10·76	11·90
66			91	2381	0·922	10·75	9·03	10·69

Reference was made in Section II to the fact that differences in K_n reflect differences in volume rather than in density of the fish, a statement which can now be substantiated. The oil content of a whole barracouta listed in Table 4 may be estimated to the nearest 1 per cent. from consideration of the percentages for different portions and the approximate fraction of the whole weight represented by each portion. In this way the range of oil content of the entire fish is found to be 1 per cent. (Nos. 26, 41) to 11 per cent. (Nos. 45, 46). The corresponding range in specific gravity may be estimated, from Taylor (1922), as 1·0743 to 1·0570. Similarly the average specific gravity, i.e. specific gravity of fish of average oil content (approximately 5 per cent., see regressions), may be estimated as 1·0674.

The general expression for K_n, actual weight divided by average weight for the given length, may be expanded: (actual specific gravity/average specific gravity) × (actual volume/average volume for the given length). If there are two samples of whole fish A and B, with mean oil contents 1 and 11 per cent. respectively, the respective values of (actual specific gravity/average specific gravity) will be 1·0743/1·0674 and 1·0570/1·0674, i.e. 1·006 and 0·990. Then

$$K_n \text{ (sample } A) = 1{\cdot}006 \text{ (actual volume/average volume)}$$

and

$$K_n \text{ (sample } B) = 0{\cdot}990 \text{ (actual volume/average volume).}$$

It follows that for any pair of K_n values with ratio higher/lower less than the ratio 1·006/0·990, the difference may be variously interpreted: (1) no change in volume relative to the average for the length of the fish (expected volume); or changes in volume relative to expected volume, either (2) the higher volume for the fish with the lower K_n or (3) the higher volume for the fish with the higher K_n. If the ratio of the K_n values is exactly 1·006/0·990 interpretations (1) and (3) are possible. But for any pair of more widely separated K_n values only interpretation (3) can hold, and differences in K_n as large as those discussed in Section IV must mainly reflect corresponding differences in volume, with differences in density having a negligible effect. Furthermore, even when the ratio is less than 1·006/0·990, interpretation (3) would very often be justified, because it is improbable that such extreme values of oil content as 1 and 11 per cent. would frequently occur, as mean values for samples of the size discussed in Section IV (see Tables 2 and 3), in such a short range of K_n values, in view of the correlations and regressions mentioned above. In any event the differences in mean K_n to which significance was attached in Section IV are all larger, mostly much larger, than those just discussed, with the exception of those from January through March 1954.

The changes in condition which are the subject of this paper are therefore for all practical purposes changes in the volume (bulk) of the fish, relative to the volumes expected for fish of those particular lengths: the better-conditioned fish weigh more on average because they are plumper than average, and the poorer-conditioned fish weigh less because they are leaner, as indicated in Section II.

VI. Occurrence of Parasitized Barracouta

Before proceeding to discuss the pattern of time changes in mean condition factor during the year, which remains evident even when allowance is made for time changes in the sexual condition of the fish in the population (Section IV(c)), it is desirable to examine the possibility that some of the changes may be due to variations in the proportion of parasitized fish in the samples studied.

The barracouta in Australian waters is host to the following parasites:

Sporozoa: *Chloromyxum thyrsites* Gilchrist (Gilchrist 1924; Willis 1949);

Cestoda: *Tetrarhynchus* four spp., *Sparganum* sp., *Ichthyotaenia* sp. (Johnston 1909);

Nematoda: *Stomachus* sp., probably *S. marinus* (L.) (Johnston and Mawson 1951);

Acanthocephala: *Echinorhynchus* sp. (Johnston 1909);

Trematoda: *Winkenthughesia thyrsites* (Hughes) (Sproston 1946), *Capiatestes thyrsitae* Crowcroft (Crowcroft 1948).

Chloromyxum occurs in the trunk muscles where it is responsible for the condition known as "milkiness" (Willis 1949). Two of the species of *Tetrarhynchus* also occur in the trunk muscles and barracouta so infected are called "wormy". *Chloromyxum* and *Tetrarhynchus* cause significant losses to barracouta fishermen. The other species all occur in parts of the body which are removed or cleaned shortly after the fish is caught: two species of *Tetrarhynchus* in and on the intestinal coats, mesentery, and peritoneum; *Sparganum* in the intestinal coat; *Ichthyotaenia* in the intestine; *Echinorhynchus* in the intestinal walls; *Stomachus* on the mesentery; and *Winkenthughesia* and *Capiatestes* on the gills.

Barracouta fishermen are much concerned with variations in the proportions of milky and wormy fish in their catches and variously consider them to be related to differences in fishing area, time of year, and size and condition of the fish. Scientific information is lacking. Data on milky fish are particularly hard to obtain because the condition (liquefaction of the muscles) generally does not become conspicuous until 12–24 hours after death, when the fish are usually on their way to market.

During the barracouta investigations 39 samples of southern Victorian and 12 of south-east Tasmanian fish were kept on deck for about 24 hours after all other observations had been made on them, and then re-examined for signs of milkiness; indications of worminess were noted at the same time. This was done as a fisherman would do it, merely by examining all surfaces and feeling the flesh for indications of local softness, and it is quite possible that some affected fish were not detected.

For the southern Victorian samples the percentage of fish in the milky condition was nil in seven samples, from 1 to 4 in eleven, from 5 to 9 in eight, from 10 to 24 in twelve, and 100 in one. Although the data warrant a more detailed study than it is convenient to present here, it may be said that they show no obvious relationship between percentage of sample showing milkiness and area, year, time of year, mean size of fish, or mean K_n. It was especially noticeable that the mean K_n of milky fish was generally close to that of non-milky fish in the same sample. Of the twelve south-east Tasmanian samples there were five in which the percentage milky was nil, six in which it was from 1 to 4, and one in which it was 30. These observations agree with the general impression, obtained from interviews with fishermen in various Victorian and Tasmanian ports, that about 5–7 per cent. of all fish caught become milky and that high percentages are unusual and transitory.

The percentages of fish in the wormy condition in southern Victorian samples were as follows: nil in 24 samples, from 1 to 4 in nine, from 5 to 9 in two, from 10 to 23 in four. For the south-east Tasmanian samples the percentages were quite different, namely: nil in one sample, from 1 to 4 in one, from 5 to 9 in two, from 10 to 24 in three, and from 25 to 38 in five. It is quite clear that the difference is associated with the larger average size of south-east Tasmanian fish (Blackburn and

Gartner 1954), since the wormy individuals of both regions were large: of 162 that were measured 150 were 80 cm or over and only two were under 70 cm (66, 67 cm). Presumably the chances of becoming parasitized by cestodes in the muscles increase as the fish ages. In the waters of South Australia and Western Australia, where barracouta are also large, there are frequent reports of worminess in this species. Neither in the Victorian nor the Tasmanian material was any relationship observable between percentage of fish in the wormy condition and area, year, time of year, or mean K_n; K_n was generally about the same for wormy and non-wormy fish in the same sample.

A further indication that variations in the percentage of fish with milkiness are independent of variations in K_n is provided by a set of data made available by a fish company which handles southern Victorian barracouta. The data consist of percentages of total receivals by weight which were rejected because of milkiness, for the successive months March through May 1950, January through May 1952, and November 1952 through February 1953. The percentage was fairly constant, from 2·0 to 3·4, until the last four months when it was successively 7·1, 12·2, 13·5, and 13·7. Figure 2 shows that mean K_n fluctuated much more and in an entirely different way during those periods.

The possibility that seasonal (or annual) fluctuations in condition depend upon the occurrence of parasites in the trunk muscle is therefore denied. Nothing is known about the extent to which the other parasites occur in barracouta populations.

VII. Discussion

The most interesting of the abovementioned results is the succession of highs and lows of condition, three of each within the year, described in Section IV(*a*). Such variability is unusual: the pattern usually described by fisheries biologists is one low and one high per year (Thompson 1943; Hart 1946), although two of each have been noted (Ellis and Gowing 1957; Qasim 1957).

In many of the instances in which only one low and one high were noted it was possible for the investigators to explain the annual cycle of condition very largely, although seldom completely, by the sexual cycle. This was done by Thompson (1943, p. 196) for the plaice, *Pleuronectes platessa*, in which the high and low occur respectively just before and just after spawning.

Other sets of observations demanded more complex explanations. For instance Hickling (1945) with the Cornish pilchard, *Sardina pilchardus*, found the low of condition before the spawning season and the high after it, which he explained by the sexual cycle and the cycle of availability of food: both breeding and feeding are at a peak in summer, when the food supply permits the pilchard not only to ripen its gonads but also to accumulate reserves of fat to sustain it through the following year.

For the barracouta of southern Victorian waters it has been shown that the principal feeding season is from late spring through summer (Blackburn 1957), about the same time as the spawning season (Blackburn and Gartner 1954); and that the level of condition is high just before this period, first low and then high during it, and low just after it (spring high through autumn low), with further fluctuations occurring in the colder months (Section IV(*a*)). These observations defy any explanation as simple as those mentioned above, especially since it has been shown that the fluctuations in condition are similar for fish with gonads at different stages (Section IV(*c*)) and for fish with and without head and viscera (Section IV(*a*)); changes in gonad weight obviously have only a minor effect upon mean K_n.

In the light of present-day knowledge of the physiology of fishes (Brown 1957, and references there) it seems doubtful that interpretations as simple as those of Thompson and Hickling could now be advanced for many populations, and it is not surprising that it is difficult to find one for a migratory species like barracouta. The importance of other variables besides food intake and reproductive stress of the fish should be borne in mind. Starting with the amount of food consumed, which itself will vary because of changes in availability of food and appetite of the fish, it must be recognized, firstly, that only a portion, probably variable, is assimilated; secondly, that the assimilated part will be partly (or wholly) respired away by the tissues to provide energy for basal metabolism and activity (reproductive and other, e.g. migratory, activity), leaving only part (or none) for the net growth of the fish; thirdly, that growth takes place in length and in weight but not necessarily in both at the same time; and finally, that growth in weight involves change in both gonad and soma.

As far as the barracouta is concerned there is the abovementioned information about the amount of feeding in different seasons, with the important reservation that nothing is known about feeding in the Furneaux Islands region where the fish are believed to go in winter; the information about the season of reproductive activity; and the evidence that changes in weight at a given length are mainly changes in the trunk and not in the gonads, which are comparatively small in bulk. Nothing is known about seasonal changes in assimilation or in growth in length. A further difficulty is that the "balance" between maintenance and growth may vary with physico-chemical factors of the environment (e.g. temperature) and with size, age, and physiological state of the fishes (Brown 1957). It is known that there is considerable migratory activity over much of the year, with peaks probably in spring and autumn (Blackburn and Gartner 1954). These activities, and others such as seeking, herding, and capturing prey (Blackburn 1957), could well require more energy at certain seasons than the contemporaneous assimilation could provide, resulting in a drawing on reserves and a fall in condition; at other times assimilation would be more than sufficient to meet the current energy requirements and condition could improve. The fact that seasonal lows of condition are largely independent of gonad stage suggests that they reflect the energy demands of non-reproductive types of activity, of which migratory activity might well be the most important.

The situation is little better when it comes to trying to explain differences in condition from year to year, of which the most striking example is the high level for southern Victorian fish throughout 1950–51 (Section IV(*b*)): the same variables are involved, although some of them could be expected to vary less than others from year to year at the same phase of the condition cycle. One variable about which there is definite information is sea temperature, which was high from December 1950 through March 1951 compared with the same period in 1948–49, 1949–50, 1951–52, and 1952–53 (C.S.I.R.O. Aust. 1951, 1953*a*, 1953*b*, 1954: data for Port Phillip Heads in area XI). Such increase in temperature could bring about better growth (and therefore condition), and has often but not invariably been found to do so in controlled experiments with fishes (Brown 1957).

It is of interest at this point to note that barracouta taken along the southern coast of Victoria in the 1950–51 fishing season were scarcer and feeding more lightly there than usual, which has been taken to mean that they were seeking food further offshore, where supplies are often available (Blackburn 1957). The unusually high level of condition in 1950–51 strongly supports this explanation, since it is almost inconceivable that condition could have been so high if food consumption had been below normal. That is to say, the good condition of coastal fish was the result of good feeding elsewhere, where many of the fish which ordinarily would have visited the coast apparently remained. However, in 1951–52, when fish were again scarce and short of food in coastal waters, their condition was not as high as in 1950–51; temperatures were not as high either, which could have affected the food supply or the feeding activity or appetite of the fish in the offshore waters; on the other hand it is clear that towards the end of the 1951–52 season the majority of the older fish were not appearing on the coast at all (Blackburn and Gartner 1954; and Section IV(*c*) of the present paper), and for all that is known about them their condition might have been excellent.

It was hoped at the outset that this investigation might assist barracouta fishermen to catch more well-conditioned and fewer ill-conditioned fish, thereby improving not only the quantity (more flesh by weight for the same number of fish hooked) but also the quality of the catch (fat fish being preferred by man to lean in most species, including *T. atun* in South Africa). Unfortunately the annual cycle of condition of the Australian barracouta lends itself less conveniently to such rational exploitation than does the cycle of the same species in South Africa, where the "fat snoek" and "poor snoek" seasons are so distinct that fishermen can avoid the latter. There is a more complex succession of highs and lows of condition in Australian waters, at least in the important southern Victorian region, and the timing of these changes is too variable and little understood to make it possible to predict them. Generally speaking condition is better at the beginning and near the end of the fishing season than in the middle (Fig. 2), but the end is variable in time and condition may be poor even then, as it was in 1951–52. Really the only generalization that may confidently be made is that condition is good at the beginning of the season ("spring high"), which some discriminating buyers already know.

It was indicated in Section IV(*d*) that the spring high of condition may possibly be evident in late winter in the Furneaux Islands region. However that area has no significant barracouta fishery of its own and is too far from Victorian or Tasmanian barracouta ports to be fished from them with boats of the type now in use. Steam trawlers take some barracouta off the Furneaux in late winter and could probably increase their catch of that species, but there is little demand for barracouta in Sydney, the home port of these vessels.

There might eventually be some benefit to the barracouta fishery if further work were done on the oil content of heads and viscera, which are at present valueless except occasionally (heads only) as crayfish bait. As indicated in Section V, the average oil content by weight of these portions is probably about 8 per cent. in south-east Tasmania over an entire fishing season, and 9 or 10 per cent. over certain parts of the season when the fish are heaviest for their length: no data are available for Victorian fish. If all the heads and viscera from several ports could be brought to a single place it might, under certain economic circumstances, be found worth while to process them into oil and meal. The annual catch of headless cleaned barracouta on the south coast of Victoria (areas IX, X, XI, XII) averaged about 4·1 million lb over the period 1947–48 through 1953–54 (Blackburn 1957); and as the ratio of headless cleaned weight to round weight is about 7 : 10 the average weight of heads and viscera obtained annually over the period may be estimated at about 1·8 million lb or 800 long tons. The corresponding average for eastern Tasmania (areas I, II, III, IV) over the same period may be estimated at slightly over 400 tons. The chances of profitably processing these rather small quantities would be brightest if they could be delivered to a reduction plant already in operation, e.g. on whales. The fish offal could be preserved with dilute formaldehyde, or sodium nitrite (Anon. 1951), or both, or with dilute alkali (Reay 1950, and references there) while awaiting reduction.

VIII. Acknowledgments

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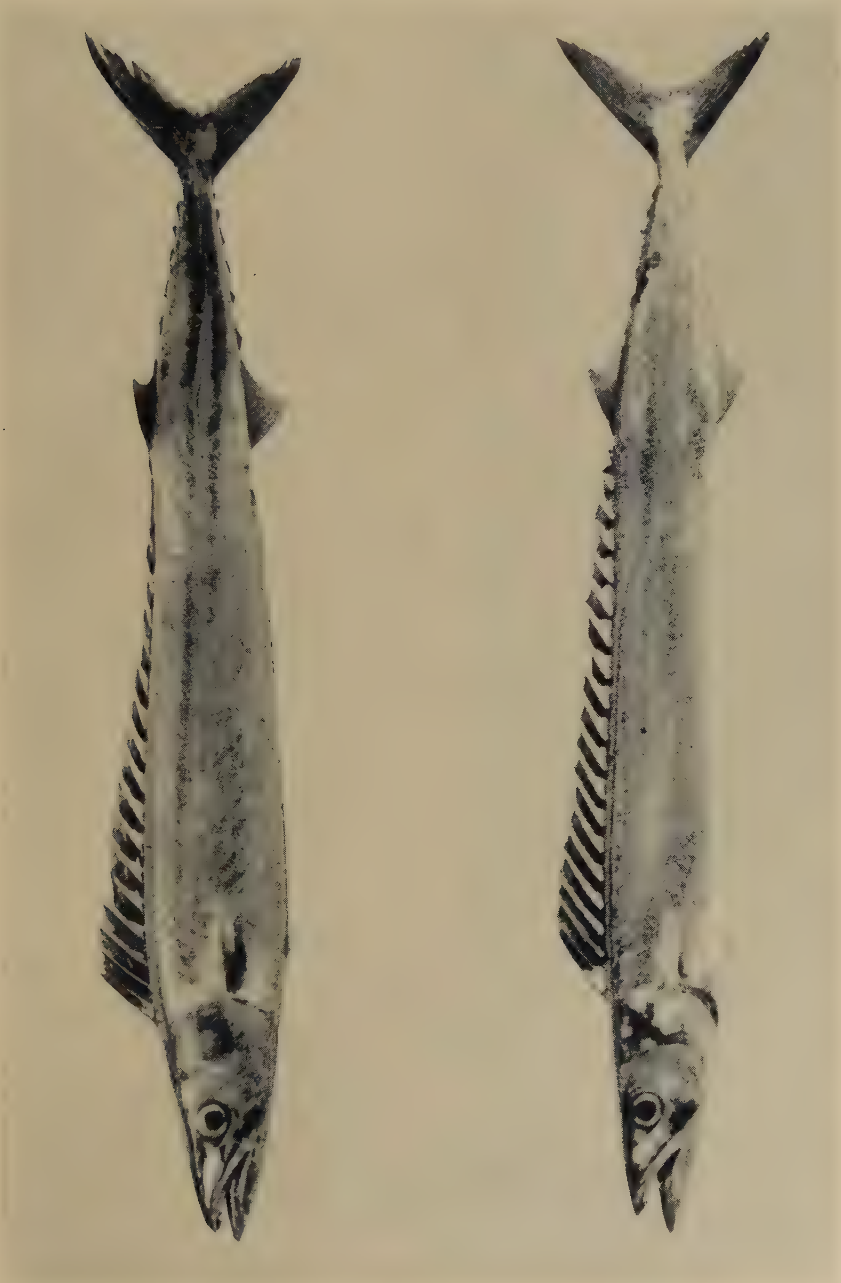
CONDITION OF AUSTRALIAN BARRACOUTA



(a) (b)

Australian barracouta, (a) $K_n = 1\cdot101$ and (b) $K_n = 0\cdot866$.

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EXPERIMENTS ON REARING THE BARNACLE *ELMINIUS MODESTUS* DARWIN TO THE SETTLING STAGE IN THE LABORATORY

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Summary

Nauplii from freshly collected adults were fed with the diatom *Phaeodactylum tricornutum* Bohlin and dried liver powder in mass culture tanks. Details of the method of preparation of food, design of the tank, rate of flow of sea-water, and population densities are given. Low but consistent yields (0·02–3·80 per cent.) of settling cyprids were obtained, the total from five consecutive experiments being 3431. At the locality (Menai Straits, North Wales) natural settling of *Elminius modestus* Darwin took place in the summer months (May–September) with a main peak about June–July. The above experiments were made during winter (December–March) when natural settling was not detected on exposure plates immersed concurrently in the sea amongst adults of this species.

I. Introduction

Observations on the settling of many marine invertebrate larvae are usually made during the natural settlement season. Even when the breeding season is of short duration it is often possible, particularly in species having planktotrophic development, to obtain very large numbers of early developmental stages. Thereafter the main difficulty is to provide suitable food and rearing conditions during planktonic life so that a yield of healthy settling stages results. Failures are commonly attributed to initial unhealthiness of the early stages, unsuitable food, or the accumulation of toxins in the culture dishes. By using the method outlined below it was found possible to produce small but consistent yields of settling cyprids of *Elminius modestus*, even though the work was carried out during winter when natural settling was not taking place and the metabolism of the adults was at its lowest level. While further work is needed to improve the yield, the method already seems suitable for mass culture of the cyprids of this species, and possibly others, and may therefore be of interest to those engaged in similar studies.

II. Availability and Collection of Nauplii

E. modestus was selected for study because it has nauplii available throughout the year, is quite widely distributed in certain regions of both hemispheres, and, since it occurs high in the intertidal zone, is usually easily obtained. The larval stages have been described (Knight-Jones and Waugh 1949). Breeding tends to be continuous and under favourable conditions settling can take place over a considerable part of the year. In New Zealand, Moore (1944) noted eyed nauplii in egg masses at all seasons of the year and Skerman (1958) recorded newly settled

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stages (or cyprids) at several of the ports over most of the year. In Britain the reproductive season is longer than that of any other barnacle present (Crisp and Chipperfield 1948) and breeding can take place at any season provided the temperature does not fall below 6°C and the food supply is adequate (Crisp and Davies 1955). It is the only barnacle in Britain which has egg masses from which first-stage nauplii can be obtained throughout the year (Crisp 1957). The settling season in south-east England extends from May to September with a main peak about June or early July (Knight-Jones and Waugh 1949; Knight-Jones and Stephenson 1950). The settling season is essentially similar in the Menai Straits, North Wales, but the settlement is less heavy. After the main settling season (June–July) there was a decline in numbers settling on exposure plates during August and September. No settlement was detected during the experimental period (December–March) on grooved "Tufnol" surfaces placed amongst adults at the Menai Bridge Pier. Adults used as naupliar sources in the work were collected from here or the nearby Bangor Pier. Large numbers of nauplii seemed available at any time; Table 1 shows counts made on nauplii taken from small collections of adults made at various times and substantiates Crisp's (1957) observation that nauplii are available throughout the year in certain parts of the British coast. The midwinter sample of *Elminius* (Feb. 11) shown in the adult tank in Plate 1, for instance, released 250,000 nauplii on the first day in the laboratory, 125,000 on the second, and 150,000 on the third, and totalled over 500,000 in the first week. The seawater temperatures for the preceding 6 weeks averaged 5·7°C (daily readings) which was close to the critical lower limit (6°C) for reproductive activity given by Crisp and Davies (1955), hence the embryos present had probably been in the adults for more than 6 weeks. Nauplii for experiments were most conveniently obtained from undamaged adults immediately after they had been brought into the laboratory. Clusters of mussels which were richly encrusted with *Elminius* were removed from the piers, washed with seawater, and placed in bituminous coated wire netting trays which were suspended in a large glass tank (60 by 30 by 30 cm) of slow running aerated seawater (Plate 1). The temperature of this tank was not controlled and was usually 12–15°C, some 5–7°C higher than the current sea temperatures. Nauplii were released from the adults in the tank within the first few hours and usually reached a maximum in numbers on the first day. Substantial numbers were still evident on the second and third days but numbers became smaller and more irregular after that. The nauplii, being

TABLE 1

NUMBERS OF ELMINIUS MODESTUS NAUPLII OBTAINED FROM SMALL IRREGULAR-SIZED COLLECTIONS OF ADULTS AT MENAI BRIDGE

Dilution counts of fraction of total obtained

	Oct. 58				Nov. 58				Jan. 59		Feb. 59
	2	3	14	23	4	7	17	18	5	17	11 – 13
No. of nauplii (thousands)	16	87	30	21	79	96	38	50	400	33	500

strongly photopositive at liberation, swam towards a light placed at one end of the tank and concentrated there at the water surface. They were pipetted off at intervals into 500-ml measuring cylinders and samples were taken for counting before the nauplii were added to the rearing tanks. Wide-mouthed pipettes (aperture diameter 5·0 mm) were used in all transfers to avoid damaging the nauplii.

III. FOOD PREPARATION

The basic food supplied to nauplii was uni-algal, but not bacteria-free, cultures of the small diatom, *Phaeodactylum tricornutum* Bohlin, formerly known as *Nitzschia closterium* (Ehrenb.) W. Sm. forma *minutissima* Allen & Nelson. *Phaeodactylum* was selected in preference to flagellates because although it was small enough for stage II nauplii to swallow, it was too large to be ingested by the species of ciliates commonly occurring in the cultures. The ciliates were therefore prevented from multiplying rapidly, when they would have reduced the density of the food, as was noted in the rearing of the tubeworm *Hydroides norvegica* Gunnerus (Wisely 1958). The spindle-shaped normal cells (see Wilson 1946) measuring 20–30 μ in length but only 2–4 μ at the widest diameter were used. Since all sea-water lines and the circulating pump at the laboratory were made of the rubber-based plastic "Dexonite" (Dexine Ltd., London and Rochdale) the sea-water used in culture work had not come in contact with heavy metals, and was not liable to contain an amount in excess of the concentrations present in the sea. Initial stocks of *Phaeodactylum* were kindly supplied by Dr. M. Parke of the Plymouth Laboratory, and were subsequently grown in enriched sea-water and soil extract. *Phaeodactylum* will grow without soil extract (Spencer 1954) but it was considered desirable to include it in the media in case any of its constituents, such as trace elements, were essential to the nauplii. Counts of *Phaeodactylum* were made with a haemocytometer.

Stock solutions of soil extract were prepared by boiling, in an enamel bucket, equal volumes of rich garden soil and tapwater for 15 min, followed by filtering with a Whatman's No. 1 filter paper. The amber-yellow filtrate was placed in flasks and heated to 100°C. The flasks were plugged with cotton wool, and allowed to cool to 20–30°C. At this stage the filtrate was enriched with phosphate and nitrate; 0·2 g of sodium nitrate and 0·02 g of anhydrous disodium hydrogen phosphate (reagent grade) were added to each 50 ml of soil extract and the flasks replugged. Stocks prepared this way remained suitable for use for several months and were added to filtered sea-water and inoculated with *Phaeodactylum* as required. The *Phaeodactylum* was grown in vigorously aerated 2, 10, or 25 l. glass containers of filtered sea-water to which was added 50 ml of the soil extract per litre of sea-water and a large (10–20 per cent. by volume) inoculum of a *Phaeodactylum* culture. Illumination was supplied by 150-W bulbs at room temperature (8–24°C). Glassware was washed in hot water and "Teepol" detergent and sterilization was not used. Cultures could be put down rapidly and were usually sufficiently dense for use ($>$1,000,000 free cells/ml) in 7–10 days.

Dried liver powder was used as a supplementary diet and the present author is grateful to Dr. C. P. Spencer for suggesting the following method of preparing it. About 250 g of fresh, finely minced sheep liver was slowly added to briskly stirred acetone at room temperature and then stored at 0°C for an hour. It was then placed in a Whatman's No. 1 filter paper in a large Buchner funnel connected to a suction pump and washed with three changes of 50 per cent. acetone and ether, followed by one change of ether. The resulting powder was dried for 2 days in a desiccator over phosphorus pentoxide and ground up using glass beads in a shaking machine; the fraction passing through a coarse plankton net (hole diameter 0·25 mm) was stored in screw-topped jars and showed excellent keeping properties. One preparation was ample for several months' feeding. Some difficulty was encountered in making suitable suspensions of the powder in sea-water. Shaking and stirring resulted in the particles clumping, owing to stickiness produced by wetting. Nauplii swimming through such suspensions soon became coated, particularly at the bases of the appendages, with clumps of particles which slowed them down and seemed likely to decrease their feeding efficiency. It seemed necessary to introduce the liver into the rearing tanks as discretely separated particles. Sieving the powder through a fine plankton net gave better results but much of it was lost to the surrounding air before making contact with the water. Improvement was noted when the modified pipette shown in Figure 1 was used. As this was worked over the surface of the water the air pressure generated from the bulb forced the liver powder in the barrel out through the plankton net at the end with considerable velocity. The particles gave rise to a surface film on touching the water surface and the spreading of this film isolated each particle until it had absorbed sufficient water to enable it to sink in the tank amongst the nauplii. Thus only particles small enough to be utilized were added, clumping and its detrimental effects were minimized, and the nauplii did not have access to the particles until they had become softened by water absorption. Weighing the pipette before and after feeding gave an approximation of the amount added, although this was still subject to some error by the loss of particles to the surrounding air. Usually about 0·01–0·02 g was given to the nauplii thrice daily.

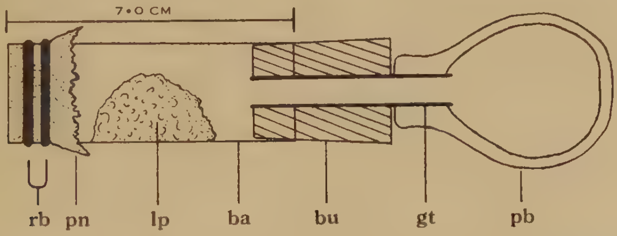

Fig. 1.—Diagram of pipette used to add liver powder to rearing tanks. *ba*, Barrel (cut from plastic tubing); *bu*, rubber bung; *gt*, glass tube; *lp*, liver powder; *pb*, pipette bulb; *pn*, piece of fine plankton net (200 mesh; hole diameter approx. 60 μ); *rb*, rubber bands.

IV. Design of Rearing Tank and Accessories

The disadvantage of using finger bowls or similar containers for rearing larvae is that noxious substances emanating from dead larvae, unused non-living food, or excretory products are liable to accumulate; this necessitates filtering off the larvae every few days, cleansing the containers, and changing the water. To avoid the risk of sudden drastic mortality larval densities are kept low. If running water is employed the fine filters needed to retain the larvae are liable to clog. The tanks used here were designed to reduce these difficulties, the basic features being shown in Figure 2. Filtered sea-water leaves a constant-level source (*cls*) via the lead (*ll*) and control screwclamp (*g*). *Phaeodactylum* culture (*ps*) siphons down a corresponding lead and clamp (*pl*, *g*). These two drip into the rearing tank (*rt*) and are mixed and circulated by a diffusion block aerator (*a*) before leaving through the filtering sand layer in the floor of the tank (*sa*) and its supporting glass wool (*gw*) and bed of small stones (*st*). Drainage takes place through the outlet tube (*lo*) whose free end is adjusted to a height that gives a suitable water level within the tube; the filtering area is sufficiently large to allow water to percolate steadily without excessive damming up before flowing out. The rate of change of the water in the tank, assuming good mixing, is determined entirely by the incoming flow rates of the sea-water and *Phaeodactylum* and the volume of the tank.

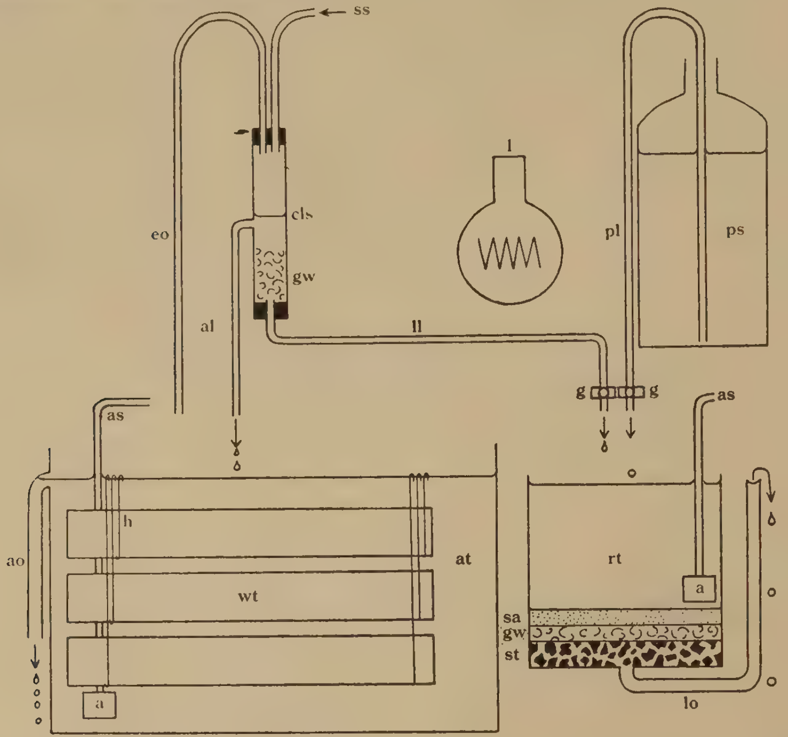

Fig. 2.—Diagram of rearing tank and accessories, not to scale. *a*, Aerator; *al*, sea-water lead to adult tank; *ao*, adult tank outlet; *as*, air supply; *at*, adult tank; *cls*, constant-level sea-water source; *eo*, emergency overflow; *g*, control screw clamp; *gw*, glass wool; *h*, hook; *l*, light bulb; *lo*, rearing tank outlet; *ll*, sea-water lead to rearing tank; *pl*, *Phaeodactylum* feed leads; *ps*, *Phaeodactylum* supply; *rt*, rearing tank; *sa*, sand layer; *ss*, sea-water supply; *st*, stone layer; *wt*, wire trays holding adults.

Nauplii placed in such a tank cannot escape through the sand layer, but toxins produced by dead larvae, unused liver powder, or other sources can do so. Moreover dead matter of this kind sinks to the bottom so the decay products are not dispersed throughout the tank but are immediately lost into the bed. The particular tanks shown in Plate 1 measured 30 by 20 by 20 cm and had a working capacity of 7 l. Each had a 1·0 cm diameter hole bored in the bottom and a length of similar diameter polyvinyl tubing fitted into this hole; the inner end of the tubing was warmed and flattened before cooling to form a retaining flange on the inside and the free end was hooked on to the outside of the tank. About 3·0 cm of small stones were first placed on the bottom (Fig. 2, *st*), followed by a 2·0 cm layer of glass wool (*gw*). Sea-water was added, the bubbles largely worked out of the glass wool and a 2·0 cm layer of coarse washed sand (*sa*) added. The tank was then filled and the height of the outlet tube adjusted to give the requisite water level. The constant-level source used was made from a 18·0 by 2·5 cm glass tube with side arm. Sea-water for the larval tank was filtered through a wad of glass wool (*gw*) (to remove silt particles) and left from the bottom; the side arm supplied the adult tank (*at*). At the top of the constant-level source were the inlet (*ss*) and an emergency outlet (*eo*) to take the abnormally high flow rates arising from the main sea-water system after pumping to capacity.

V. Outline of Rearing Method

Mass cultures of *Phaeodactylum* were started about 7–10 days before it was intended to rear larvae. Adult barnacles were then brought into the laboratory and the nauplii collected and transferred to 500-ml measuring cylinders as already described. After shaking to disperse the larvae evenly, six 0·1 ml samples were drawn off each cylinder and the nauplii in them fixed and counted to obtain an estimate of the number present. The rearing tanks were partially emptied before adding nauplii and the drip feeds started so that the water level began to rise; this prevented nauplii becoming stranded on the sides of the tank. The black band of adhesive tape adequately covering the waterline in the tanks (Plate 1) was introduced for the same reason, for without it nauplii concentrated in the meniscus at waterline and some became stranded on the walls by the slight waves originating from the aerator. Since the flow rates were slow, the temperature of the tank soon approximated that of the room, which was maintained between 17 and 23°C. Representative flow rates, densities, etc. are given later. Small alterations were often made daily to these after examining a sample of nauplii. Healthy larvae were extremely active and their alimentary canals were filled with *Phaeodactylum* and liver particles. Sluggishness of the larvae was often indicative of impending mortality but the reasons for this were not always apparent. Sometimes it appeared to be due to underfeeding; the alimentary canals were only partially filled and increasing the food supply resulted in many of the larvae feeding and swimming much more actively. At other times it appeared to be due to excess liver powder and bacteria in the tanks, caused by inadequate sea-water flow. Fine strands of bacterial slime with attached particles could be seen adhering to the nauplii (particularly to their appendages) and in extreme cases caused nauplii to stick to the tank walls in large numbers, or to one another. Unless this was detected very early it was of little value to increase the sea-water flow. Unusually large concentrations of dead nauplii often appeared about the fifth day when most of the nauplii were moulting to stage IV and these were pipetted out of the tanks and the sea-water flow temporarily increased. In the final experiments the rearing tanks were kept mainly in darkness and this reduced the growth of algal films, particularly blue-green species, which were liable to form on the sand and tank walls during the second week of rearing, encouraged no doubt by the nitrogenous matter from uneaten food. These, like bacterial films, were undesirable since nauplii became stuck to them and were unable to feed properly. The first cyprids usually appeared after 16–18 days and reached a peak in numbers several days later. When the tanks were horizontally illuminated the cyprids concentrated mainly at the bottom and could be conveniently pipetted off as requested; if left there they settled and metamorphosed readily on the tank walls. After each batch was reared the tank walls were thoroughly scrubbed with hot water and "Teepol" detergent and the top of the sand layer was removed and replaced with fresh sand. This reduced the chances of algal contamination in the next rearing.

VI. Results

Five consecutive experiments using the above methods were carried out between December 1958 and March 1959, the rearing conditions and results being as follows:

Experiment 1.—Approximately 50,000 nauplii were placed in a rearing tank between December 8 and 11 to give an initial density of 7 nauplii/ml. Development took about 17 days at 22°C and 1902 cyprids (3·8 per cent.) settled, metamorphosed successfully, and commenced growth on the tank walls. The rearing conditions recorded during the settling period (Table 2) were representative of those used throughout this and the other experiments, but, as noted earlier, small daily alterations were often made.

Experiment 2.—Approximately 330,000 nauplii were obtained on February 18 from adults collected the previous day, to give an initial density in the rearing tanks of 47 nauplii/ml. The first cyprids appeared on the fifteenth day at 19–20°C and the total yield was 805 settled cyprids (0·24 per cent.). Despite the initial heavy density mortality was not abnormally high until the twelfth day when colonies of blue-green algae became prominent, and despite daily scrubbing with a toothbrush these continued to develop on the tank walls and to entangle large numbers of nauplii. As the growth of these algae may have been facilitated by illumination the tanks were kept in darkness in the following three experiments.

Experiment 3.—Adults collected on February 10 released 250,000 nauplii the following day. The larval density was 36/ml and development took about 20 days at 19°C to give a yield of 48 settled cyprids (0·02 per cent.). The main losses took place on the seventeenth and eighteenth day when the nauplii became sluggish. Part of the loss was due to bacteria forming on the larvae and clumping them together, but the remainder could not be accounted for.

TABLE 2

REARING CONDITIONS FOR LARVAE (SEE TEXT, EXPERIMENT 1)

Conditions	Date (Dec. 1958)							
	22	23	24	25	26	27	28	29
Sea-water temperatures (°C)								
Of sea-water source	9	9	9	9	9	9	10	9
In adult tank	14	14	15	13	14	15	16	14
In rearing tank	21	21	22	23	24	22	22	23
Flow rates (ml/hr)								
Sea-water in adult tank	7,200	6,000	6,200	6,600	6,000	6,600	6,600	6,000
Sea-water in rearing tank	340	340	340	340	208	256	256	272
Phaeodactylum into rearing tank	20	20	35	25	40	32	32	40
Phaeodactylum concentration (cells/ml)								
Of supply	1,376,000	1,760,000	1,248,000	1,648,000	1,600,000	1,136,000	1,120,000	1,360.000
In rearing tank	160,000	160,000	28,000	36,000	60,000	76,000	32,000	25,000
Daily liver powder ration to nauplii (g)	0·030	0·020	0·025	0·030	0·030	0·025	0·030	0·030
Cyprid yield to date	135	164	1,347	1,663	1,728	1,793	1,884	1,902

Experiment 4.—The second day's release of nauplii from the adults in the previous experiments were used. These totalled 125,000 to give a larval density of 18/ml. Development took 19–20 days at 19°C, the yield totalling 337 settled cyprids (0·3 per cent.). The main losses again occurred after 17–18 days, but clumping of the nauplii on the tank walls was not apparent. Settling extended over a considerable period and small numbers of cyprids were still settling on the twenty-third day.

Experiment 5.—The third day's release of nauplii (150,000) from the adults of Experiment 3 were used; the larval density was 21/ml and the yield of settled cyprids 339 (0·2 per cent.). Development was slightly faster than in the previous experiments and cyprids first appeared on the seventeenth day of rearing. Mortality occurred mainly about stage III–IV when the numbers dropped suddenly. When the adults for these three experiments were collected the sea-water temperatures, as noted earlier, were at their minimum values (5·7°C) and there had been a series of frosts for seven days. Although it is not known how viable nauplii are under such conditions, it may have been that these, coupled with the sudden increase of 15°C they experienced on entering the laboratory, had an adverse effect on them.

Clearly further work on seasonal viability, optimum temperatures and rearing conditions, effects of bacteria, and food is needed before consistent yields can be expected. Although the percentage yields of settled stages was low (0·02–3·80 per cent.) positive results were obtained and the total from the five experiments was high (3431). The availability of *Elminius* nauplii, *Phaeodactylum*, and liver powder is not restricted to any season and it seems feasible, notwithstanding the lack of basic knowledge on mortality factors, that if the present methods were used on an increased scale, it should be possible to produce continuous supplies of settling cyprids for experimental work. It has been shown that it is possible to produce settling cyprids during February (Experiments 3–5) which is probably the most difficult month of the year in Britain, and it is to be expected that yields would be higher during the natural settling season (May–September) and particularly during the peak period (June–July).

VII. Foods Used in Rearing

Costlow and Bookhout (1957, 1958) have briefly described and given references to most of the earlier work on rearing barnacles. Out of the numerous attempts reported to date there have been five where nauplii were fed and reared to the young settled stages, viz. *Balanus crenatus* Brug. (Herz 1933), *Balanus amphitrite* var. *hawaiensis* Broch (Hudinanga and Kasahara 1941), *Balanus eburneus* Gould, and *Balanus amphitrite* var. *denticulata* Broch (Costlow and Bookhout 1957, 1958), and now *Elminius modestus* Darwin. Many of the earlier workers did not include details of food, naupliar concentrations, stage reached, and yields, particularly when rearing was only partly successful, and this makes analysis of their methods difficult.

A phytoplankton diet (one of the diatoms *Skeletonema costatum* Grev. and *Phaeodactylum tricornutum* Bohlin or the flagellate *Chlamydomonas* sp.) has been a common factor in nearly all attempts. Herz (1933) does not specify his food source;

it seems to have been fresh or aged sea-water in which flagellates, algae, or diatoms may have developed. Two further cases where rearing on a phytoplankton diet was partly successful may be noted. In 1956, 6 per cent. yields of cyprids of *Balanus* (*Balanus*) *amphitrite* var. *cirratus* Darwin were obtained in 13 days at 21°C by using nauplii released by undamaged breeding adults, and placed directly into flasks of dense ($>2,000,000$ cells/ml) cultures of *Skeletonema costatum* which was growing in Miquel's solution. The nauplii were resuspended in fresh culture every fourth day. The cyprids seemed unwilling to settle on the walls of the flasks and were eventually removed and preserved. In August 1958 *Elminius modestus* nauplii obtained by crushing adults and collecting any nauplii released were placed in covered unaerated 200-ml capacity bowls of dense ($>1,000,000$ free cells/ml) cultures of *Phaeodactylum tricornutum* grown in enriched filtered sea-water and soil extract and renewed on the fifteenth day. Thirty cyprids ($<0 \cdot 1$ per cent.) were obtained in 18 days at 19°C but only four of these settled on pieces of *Mytilus* shell bearing previously settled *Elminius* which were then placed in the bowls. None settled on the glass, although cyprids readily did this in the rearing tanks used later. In September a similar experiment yielded 347 cyprids ($<0 \cdot 1$ per cent.) but *Mytilus* shells were not introduced and none of the cyprids settled on the glass walls. Evidently phytoplankton cultures can be used to feed early-stage nauplii and in some cases complete development and settling occur.

Costlow and Bookhout (1957, 1958) supplemented a basic phytoplankton diet (*Chlamydomonas* sp.) with fertilized sea urchin (*Arbacia punctulata* Lamarck) eggs and also penicillin; their yields are the best recorded, 16·3 per cent. of settled stages for *Balanus eburneus* and 12·7 per cent. for *Balanus amphitrite* var. *denticulata*. They introduced sea urchin eggs into the diet after finding they were unable to rear these species (and *Chthamalus fragilis* Darwin) beyond stage III on *Chlamydomonas* alone; they included the eggs "to furnish food of animal origin". Besides dried liver powder, several foods of animal origin were tried in the present investigation, including small clots of milk or sheep blood and mollusc and annelid eggs. Stage III and larger nauplii often grasped such objects by means of the masticatory spines at the mandibular bases and carried them round while swimming. Providing the material was sufficiently fluid, it was sucked in by pumping movements of the oesophagus. Developing eggs of the limpet *Patella vulgata* L. were pierced by the masticatory hooks on the mandibles and were readily "sucked" but unfertilized eggs of the lugworm *Arenicola marina* (L.) were grasped but could not be penetrated because of their firm pellicle and were eventually discarded. If individual *Arenicola* eggs were broken and impaled on a needle so that the contents extruded and then held in the path of a nauplius they were often seized and rapidly evacuated. Large nauplii were sometimes seen carrying smaller dead ones but seemed unable to pierce the exoskeleton. In general, observations suggested that suitable fertilized eggs possess several advantages as late-stage naupliar food. Since they are motile they are more liable to be involved in collisions with nauplii and to be seized. Unlike non-living food they are less liable to decompose and pollute the water. Once the outer layers are pierced, the fluid contents are eminently suited to the sucking action of the oesophagus and can be readily withdrawn. The food value is probably high. Because suitable eggs were not readily available throughout the year in the Menai Straits, dried liver powder was substituted; Howie (1958) has obtained promising results with this (and egg and nettle powder) in rearing annelid larvae. As noted earlier, care was taken to introduce only small water-softened particles of liver amongst the nauplii.

VIII. Use of Penicillin

Costlow and Bookhout (1957) used penicillin in their experiments because it was observed that the tendency for the nauplii to stick on surfaces of the rearing assembly was considerably reduced. A few observations were made on penicillin in the earlier stages of the present investigation. Covered, unaerated 200-ml capacity bowls of *Phaeodactylum* culture and nauplii were put down in sets of 12: six with penicillin and six as controls. The concentrations of penicillin used were 80, 170, and 350 international units added per ml of culture, as compared with Costlow's and Bookhout's (1957, 1958) 200–400 i.u./ml. After 7 days each bowl was agitated so that the nauplii were evenly distributed and 20–40 nauplii withdrawn and staged. Three 10 ml samples were taken and the number of live nauplii counted and averaged to give an estimate of the total surviving. Variation was small and the figures were

Table 3

CONDITION OF NAUPLII AFTER 7 DAYS CULTURE, WITH AND WITHOUT THE ADDITION OF PENICILLIN

Conditions and Results	Experiment *A* (Examined 31.x.58)		Experiment *B* (Examined 22.x.58)		Experiment *C* (Examined 10.x.58)	
	Controls	Experimentals	Controls	Experimentals	Controls	Experimentals
Penicillin (i.u./ml)	—	80	—	170	—	350
Initial naupliar density per ml	9	9	12	12	36	36
Phaeodactylum density (thousands of free cells per ml)	400	400	800	800	432	432
Temperature (°C)	15–18	15–18	15–19	15–19	15–18	15–18
Survival (%)	17	16	31	14	8	7
	17	22	22	21	24	5
	20	22	43	21	42	10
	14	14	24	15	32	3
	15	13	38	10	29	8
	20	14	27	13	30	1
Mean survival (%)	17	17	31	16	27	6
Survival (%) at stage I					5	5
II	3	2			40	72
III	96	97	71	89	55	23
IV	1	2	28	11	1	
V			1			
VI						

probably close to the true totals. The results are given in Table 3. The number of nauplii adhering to the bottoms of the bowls was not markedly different, irrespective of the presence or absence of penicillin. Penicillin introduced at 80 i.u./ml did not appear to have much effect, and at the higher concentrations (170–180 i.u./ml) the survival was actually less than that of the controls. Perhaps the penicillin was reducing the number of bacteria or flagellates which were in some way beneficial. Since the losses beyond stage III were arising mainly from previously dead, decomposing nauplii, the running flow tanks were introduced and the use of penicillin, which would have been costly in such a system, was not investigated further.

IX. Acknowledgments

Thanks are due to the Director of the Marine Biological Station, Dr. D. J. Crisp, for extending facilities, supervising the research, and for his interest and encouraging help. This work forms part of a programme on the biology of fouling organisms carried out in cooperation with the Royal Australian Navy.

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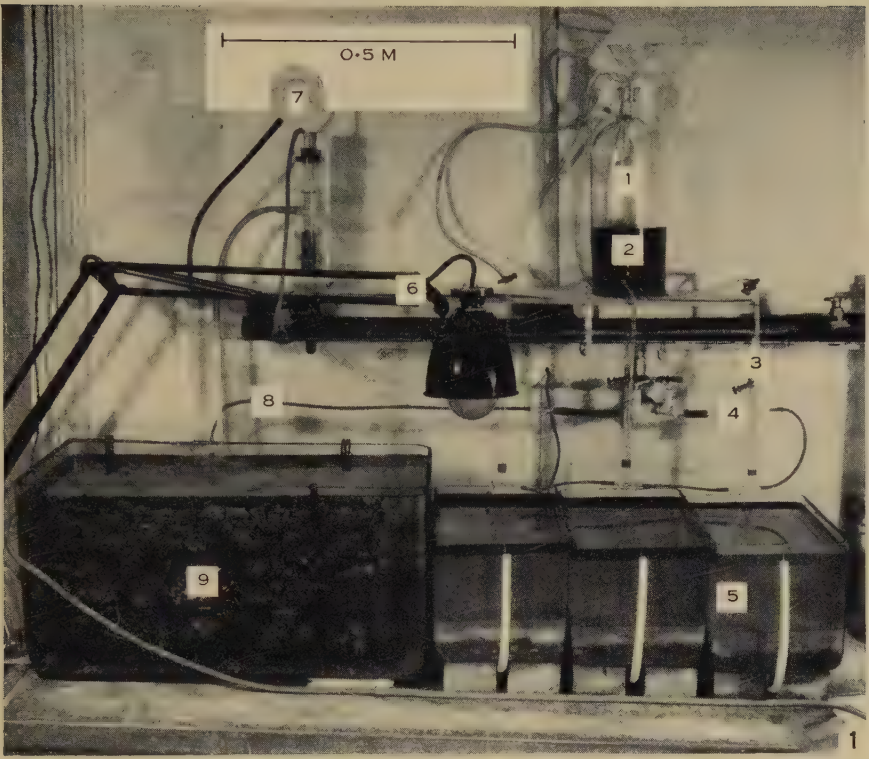
Explanation of Plate 1

Fig. 1.—General view of rearing tank and accessories. *1*, Winchester bottle of *Phaeodactylum* culture; *2*, screw clamp for adjusting rate of flow of *Phaeodactylum*; *3*, similar clamp for sea-water flow; *4*, air supply to aerators in rearing tanks; *5*, rearing tank; *6*, lamp for collecting nauplii from adults; *7*, top of side arm-tube arrangement supplying sea-water to adult and rearing tanks; *8*, air supply to aerator in adult tank; *9*, adult barnacles in wire trays.

Fig. 2.—Closer view of rearing tanks.

REARING OF ELMINIUS MODESTUS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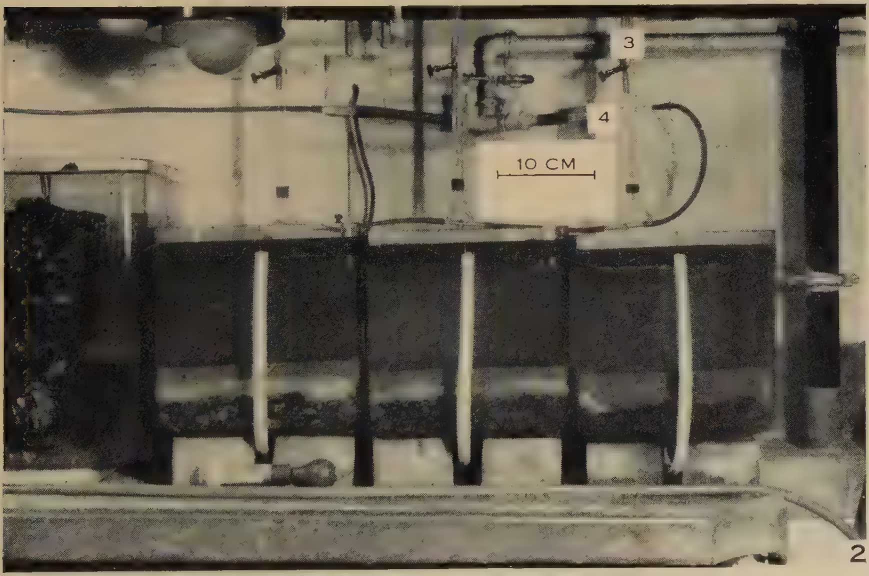

2

OBSERVATIONS ON THE SETTLING BEHAVIOUR OF LARVAE OF THE TUBEWORM *SPIRORBIS BOREALIS* DAUDIN (POLYCHAETA)

By B. Wisely*

[*Manuscript received July* 16, 1959]

Summary

Aspects of natural and experimental settling of *Spirorbis borealis* on the seaweed *Fucus serratus* L. were compared. Under natural conditions *S. borealis* appeared to settle preferentially in the concave grooves flanking the midribs, and less commonly on the flatter parts of the fronds. Settlement seldom took place on the convex midrib. The centres of individuals of dense populations, which were spaced along the grooves, were 1–2 mm from those of their nearest neighbours; none of the 2582 examined were closer than 0·5 mm. Experiments showed that larvae tended to avoid settling on *F. serratus* bearing adults of their own species, or similar shaped objects, when the density of these exceeded 10 per cm^2 and if alternative settling surfaces of *Fucus* were provided. Direct observations showed that larvae tended to explore concave areas of the fronds more intensively than other areas and turned away from nearby round, protruding objects during their final settling movements. However, larvae withheld from suitable settling surfaces for increasing periods of time showed a successive abbreviation of the pattern of searching behaviour. When they had been prevented from settling for 8 hours or more they settled on or very close to the point where they first alighted, apparently regardless of the surface contour or the presence of nearby objects. The most densely settled populations encountered naturally in the area (Menai Straits, North Wales) ranged from 12 to 33 individuals per cm^2 and averaged 21, but experimental densities of 64 to 322 individuals per cm^2 were obtained readily when larvae competed for limited settling spaces on *F. serratus* under laboratory conditions. Analysis of the settlement behaviour and its modification with the passage of time indicated how the pattern of settlement observed in nature could result.

I. Introduction

The behaviour of settling Spirorbidae larvae is of interest, since representatives of this family, although perhaps not as prominent as certain tubeworms, barnacles, bryozoans, and bivalve molluscs, are often present in fouling communities (Hutchins 1952 lists references; see also Wisely 1959). Knight-Jones (1951) has drawn attention to the suitability of larvae of the genus *Spirorbis* as experimental material; larvae of both the species he investigated were obtained readily during the breeding season, did not require feeding, and settled shortly after liberation. Their settling behaviour was complex. Amongst the more salient points recorded by Knight-Jones (1951) was evidence that larvae of *Spirorbis borealis* Daudin and *S. pagenstecheri* Quatrefages could apparently distinguish and preferred to settle among settled individuals of their own species; that *S. borealis* larvae were gregarious and settled much more commonly on pieces of *Fucus serratus* bearing a few previously settled individuals than on adjacent uncolonized pieces; and that (Knight-Jones 1953) *S. borealis*

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showed a tendency towards loss of discrimination in the choice of settling sites as settlement became delayed. In the present paper further investigations have been made using *S. borealis* collected between May and October in the Menai Straits, North Wales, where it occurs abundantly on *F. serratus* at mean low water springs. The methods used are included in the appropriate sections.

II. Natural Settling

(*a*) *Association with Concavities in* Fucus serratus *Fronds*

According to Gross and Knight-Jones (1957) about 90 per cent. of *S. borealis* in the Menai Straits occurs on *Fucus serratus*. Newly settled *S. borealis* often produce a characteristic pattern outlining the midrib (Plate 1, Fig. 1) and, though this pattern tends to persist in older populations (Plate 1, Fig. 2), it becomes less distinct as settlement spreads to the surrounding area. It also tends to outline the midrib and the bases of the globular bladders in *Fucus vesiculosus* L. (Plate 1, Figs. 3 and 4).

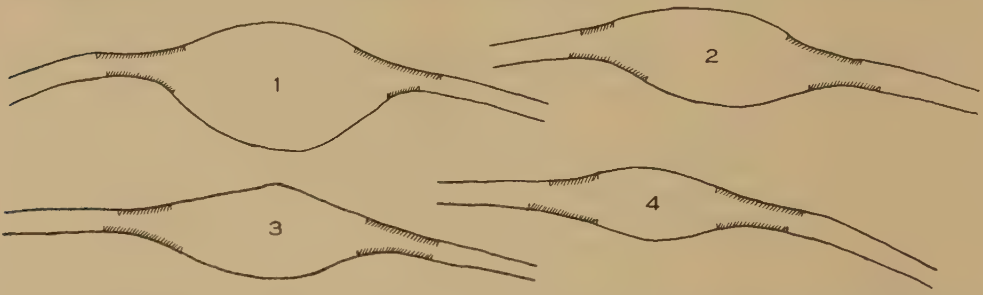

Fig. 1.—Diagrams of transverse sections of *F. serratus* midrib showing the groove areas (striped) where settlement commonly took place. *1* is representative of the basal quarter of the frond and the rest are for successive quarters. Based on camera lucida.

Transverse hand-cut sections of a frond of *F. serratus* with newly settled *S. borealis* were suspended in sea-water and drawn with a camera lucida. As the *Spirorbis* were probably less than a week old, any growth of the *Fucus* subsequent to their settlement could be expected to be confined mainly to the distal, apical cell region and it was therefore unlikely that the shape of the whole frond had altered. It was noticed that settlement had taken place most commonly in the grooves running parallel to and on each side of the midrib (Fig. 1) and this was responsible for the prominent outline of the midrib on such fronds. The arrangement in *F. vesiculosus* was essentially similar and in both species both the upper and lower surfaces of the fronds had been colonized in this way. The actual positions of settled *S. borealis* in these grooves are shown in more detail in Figure 2. In 98 out of the 100 sections it was evident that settlement had taken place in the centre of, or very close to, the most concave area available within the general area of the groove. In the other two (marked +) it had occurred on flat or slightly convex surfaces; examples of larvae settling without extensive searching behaviour are noted later and it seems possible that this occurred here. Precocious settlement may also in part account for the later colonization of the more peripheral flatter parts of the fronds, and

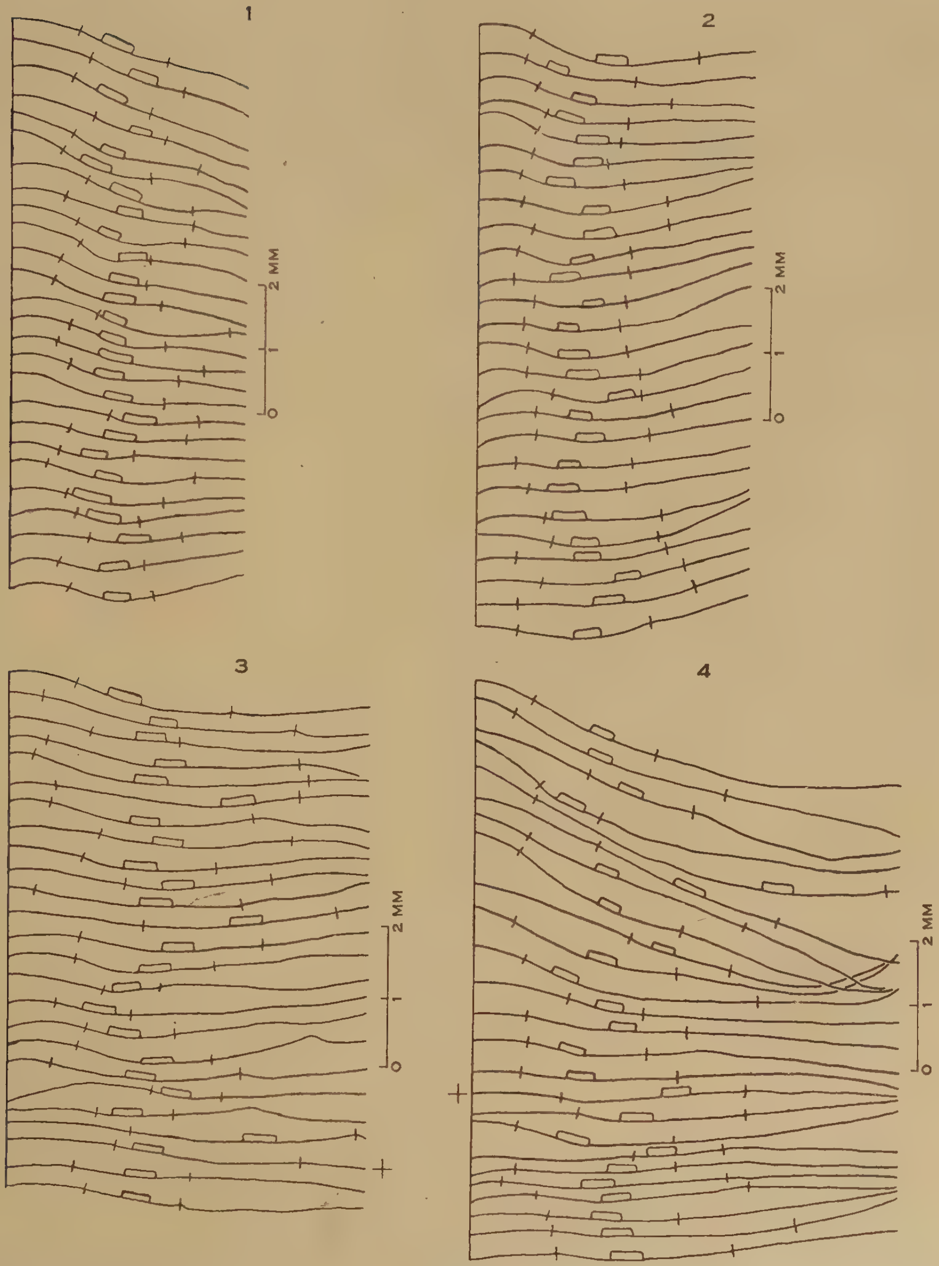

Fig. 2.—One hundred camera lucida cross sections from the upper surface of a *F. serratus* frond showing the settlement of *S. borealis* in the grooves flanking the midrib. The vertical crosslines indicate the limits of the concavities whose radial indices of curvature were determined. In each section the centre of the midrib is on the left, and all have been drawn as though they were on the right side of the midrib. *1* is a series from the basal quarter of the frond, *2* is the next quarter and so on; + denotes the two cases where settlement was on slightly convex or flattish parts of the groove.

occasionally of convex sites. The profiles of the grooves on each side of the settled *Spirorbis* were examined up to the points at which they began to lose their concavity (as indicated by the vertical crosslines in Fig. 2). In this way an approximate arc of a circle was delimited. The radii of curvature of these arcs were measured and have, for convenience here, been termed "radial indices of curvature" (r.i.c.) since they are inversely proportional to the curvature in a groove at the point of settlement and so enable comparisons to be made. *A priori*, a "deep" groove would

TABLE 1

MEASUREMENTS OF THE CONCAVITY OF GROOVES IN FRONDS OCCUPIED BY LARVAE

Frond No.	Part of Frond	No. of Determinations	Mean r.i.c. (mm)	Max. r.i.c. (mm)	Min. r.i.c. (mm)
(a) Along the Length of a Single Frond (100 Determinations)					
—	basal quarter (1)	25	2·8	5·0	0·7
—	next quarter (2)	25	3·3	5·8	1·7
—	next quarter (3)	25	5·6	8·7	2·9
—	distal quarter (4)	25	7·1	9·8	5·2
(b) For the Distal Quarters of 13 Similar Fronds (205 Determinations)					
1		25	7·1	9·8	5·2
2		19	6·7	10·3	3·6
3		18	7·4	10·3	5·7
4		11	6·2	9·7	4·1
5		12	6·7	10·3	3·4
6		19	6·4	9·4	3·4
7		14	5·4	6·2	4·3
8		11	4·2	5·3	3·4
9		23	6·6	10·6	4·2
10		13	4·7	6·5	3·1
11		14	6·6	8·3	5·1
12		13	6·1	8·8	2·6
13		13	6·4	9·0	3·5

have a low radial index of curvature (r.i.c. value) expressed in millimeters and a "shallow" groove a high value. The r.i.c. values in the above cases (Table 1(*a*)) showed that the grooves were becoming more shallow towards the distal end of the frond, as is also apparent in Figures 1 and 2. In the basal region of the frond where the grooves were deep and relatively well defined, the larvae had settled almost in a straight line along them, but in the shallower grooves near the end of the frond, settlement was not as linear. Although these grooves at the end of the frond were decidedly shallow (mean r.i.c. 7·1 mm) settlement, although less dense, had apparently taken place in them rather than on the immediately adjacent areas and a linear arrangement was still apparent (see distal end of frond in Plate 1, Fig. 1).

The r.i.c. values for the distal ends of 13 similar fronds with newly settled *Spirorbis* were determined (Table 1(*b*)) and indicated that settlement in such shallow grooves (mean r.i.c. 6·0–7·0 mm) was quite common.

This (and later evidence) suggested that there was a marked tendency for *S. borealis* to settle in concavities as opposed to flat or convex surfaces, provided they had access to them shortly (within 4–5 hours) after liberation. No obvious morphological differences were detected between the superficial *F. serratus* cells in the grooves and those nearby. The possibility that the larvae could appreciate the slightly darker colour of *F. serratus* midribs and were settling alongside did not appear to be borne out by consideration of their settling elsewhere. They settled around the grooved bases of the globular bladders of *F. vesiculosus* and abundantly in the numerous concavities present over the surface of the reproductive fronds of both species. It was noted that they could distinguish, and settled preferentially on, the more concave sides of a piece of *F. serratus*, which did not contain a section of midrib. Lastly, they settled at the concave angle between the base and the sides of "filmed" crystallizing bowls. Knight-Jones (1951) noted that "settlement took place very frequently in concavities, such as the slight grooves along the midrib of *Fucus* or the angle at the periphery of a beaker's base", and suggested that "this was probably a response to contact stimuli". Little can be added to this beyond pointing out that the presence of a midrib is not necessary and the larvae seem to be capable of distinguishing convex, flat, or concave surfaces, preferring the latter. How such a small larva can appreciate that it is in such a relatively large depression as the groove itself, and can furthermore, in many cases, apparently select the most concave part of the groove, is not understood. In this connection larvae of the bryozoan *Bugula neritina* L. show a tendency to settle at the concave angle between the base and the sides of experimental dishes (unpublished data), and Ryland (1959) noted that the bryozoan *Celleporella hyalina* (L.) preferred to settle in concavities in algae. This may, in part, explain how larvae of this species, when offered several algae on which to settle, including the species on which they were usually found in nature, did not always prefer the latter. The somewhat anomalous results obtained by Gross and Knight-Jones (1957) when comparing the settlement of *S. borealis* on algae in the laboratory and in nature, may be partly due to this behaviour. Crisp and Barnes (1954) reported preferential settlement by barnacle cyprids in suitable pits and grooves.

(*b*) *Distances between Individuals in* Fucus serratus *Grooves*

On densely settled *F. serratus* the spacing of individuals in the grooves often showed indications of regularity. A series of rather evenly spaced individuals was often followed by a blank space and then another series and so on. Such a series might consist of from 20 to 70 individuals and the blank spaces were apparently where no settling had taken place, or where it had been interrupted by rips in the frond or the presence of a fork in the midrib. If the settlement had taken place at random, irrespective of the presence of previously settled individuals, it would have been expected that at least some individuals in such series would have settled very close to one another. Measurements were made on undamaged, straight basal parts of fronds immersed in sea-water and lightly flattened under thin glass. The distances between the centres of living *S. borealis* (or remains) were measured with a calibrated eyepiece in a dissecting microscope. Accuracy was of the order of ±0·06 mm. Data for groups whose average distance apart was 1·40–1·60 and 2·00–2·30 mm are summarized in Figure 3. On such densely settled *Fucus* the centres of the majority of individuals in the grooves lay about 1–2 mm from those of their nearest neighbours, the regularity of this distance being shown by the pronounced peaks; moreover, none of the centres of adjacent individuals were closer than 0·5 mm. This was also true of a further 1132 individuals measured in other groups.

The possibility that these spatial arrangements resulted from post-settling movements is remote. It was noticed that when a *S. borealis* larva settled (even if it died 12–24 hours later) it secreted a J-shaped or spiral calcareous tube on the settling site. This had notable persistency and it was not found possible to remove it properly with a needle without taking the underlying *Fucus* cells with it, thus leaving a scar. In successfully settled individuals growth proceeded spirally and the larval settling sites persisted and coincided closely with the centre of the growing tubes. Occasionally two individuals pressed against each other during later growth and in such cases the centres of the tubes did not move over the substratum as do the membraneous bases of certain barnacles in crowded conditions (Crisp, personal communication). Instead, the growing peripheral ends of the tubes by-passed or overlapped each other. Examples of this were found in extremely dense natural

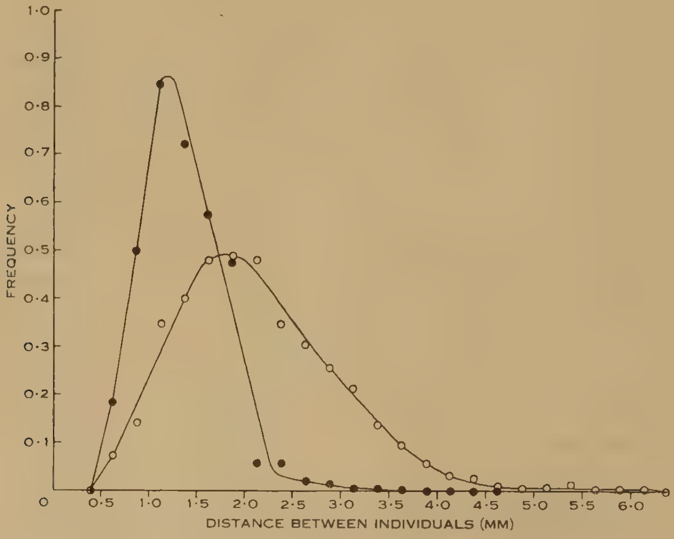

Fig. 3.—Frequencies of the distances apart between 1450 *S. borealis* in the grooves flanking the midribs of *F. serratus* fronds. ● is for 10 series whose mean distance apart between the centre of individuals was, for each series, between 1·40 and 1·60 mm; ○ is for 25 series whose means were between 2·00 and 2·30 mm (see text).

populations, but were not common. In view of this, it appeared likely that the settling sites were completely determined by the larval behaviour at settling.

(c) *Maximum Settling Densities*

The maximum settling density in natural conditions in the Menai Straits was estimated from 100 of the most densely settled fronds encountered during the entire collecting period (May–October). On such fronds the grooves and flatter parts were well colonized; the number of *S. borealis* on the most heavily settled square centimetre of each frond was recorded irrespective of its position on the frond. The numbers ranged from 12 to 33 individuals per cm^2 and averaged 21.

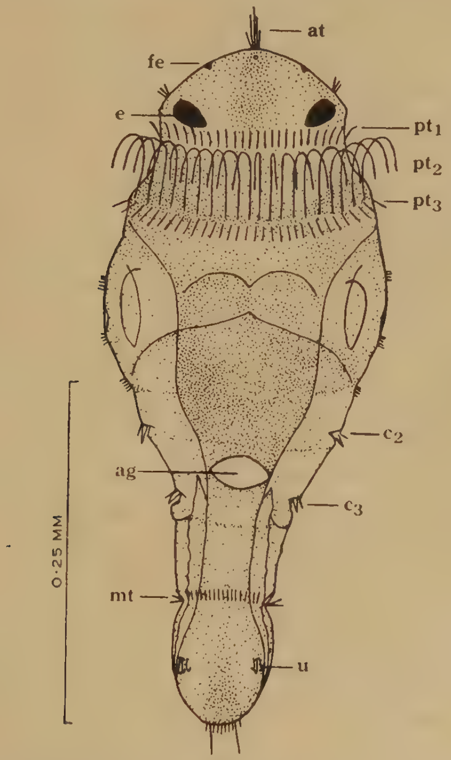

Fig. 4.—Dorsal view of a *S. borealis* larva, including structures mentioned in the text. *ag*, Attachment gland; *at*, apical tuft; c_{2-3} chaetae (c_1 was not visible in this specimen); *e*, eyespots, *fe*, frontal eyespots; *mt*, metatroch; pt_{1-3}, prototroch; *u*, uncini. Twenty-seven larvae averaged 0·6 mm length (range 0·88–0·56 mm). Camera lucida.

III. Experimental Settling

(a) *Method*

Larvae were obtained from mature *S. borealis* (diameter *c.* 20 mm) which were collected between May and October. *F. serratus* fronds bearing the adults were placed in large tanks (60 by 30 by 30 cm) of running sea-water. Adults ready to release larvae usually did so on the first and second morning after collecting; the larvae were concentrated towards the side of the tank under the influence of a 150-W bulb and transferred with a wide-mouthed pipette (aperture diameter *c.* 0·5 mm) to 95 mm diameter Petri dishes containing 40 ml of filtered sea-water. The general appearance of a larva, showing the structures referred to later, is shown in Figure 4. Höglund (1951) did not consider *S. borealis* larvae possessed a metatroch, but those examined in the present paper definitely possessed one (Fig. 4, *mt*). The first pair of chaetae were not visible in this particular specimen and have not been included in the drawing. The settling surfaces used consisted of rectangles cut from *F. serratus* fronds, or disks punched out with a modified cork borer; these were prepared several days before use and kept in running sea-water to disperse the mucus released at the cut edges, which was liable to entangle the larvae. These surfaces were also lightly wiped before use. Care was taken to use only healthly larvae, and to secure as flat and as uniform a series of settling surfaces as possible in each experiment.

(*b*) *Experimentally Induced, Heavy Settling Densities*

In these experiments large numbers (98–533) of larvae were put into a series of clean dishes, each containing a relatively small rectangle of *F. serratus* (0·675–1·465 cm^2) at 13–14°C in dim light, i.e. where the reflection from the surfaces of the dishes, as measured with a Weston exposure meter, was 17 candles per sq. ft. The larvae were thus offered the choice of settling very close together on the *Fucus*, which was the most suitable surface offered, or of settling elsewhere in the dishes. The other available surfaces were the surface film of the sea-water and the walls of the container. As noted by Fewkes (1885), these larvae can settle and metamorphose on the surface film, especially if they are kept in the dark and there is a bacterial scum (Knight-Jones 1951). The latter also recorded a 15 per cent. settlement on clean glass beaker walls, as compared with 91 per cent. for the more attractive "filmed" glass. In the present experiments the numbers of larvae settling on the *Fucus*, clean dish walls, surface film, or remaining unsettled were counted after 24 hours and from these figures the possible and the actual density per unit area of *Fucus* were obtained. The larvae used in these experiments were released and put into the dishes in the morning (0900–1000 hr) but substantial numbers were still settling in the late afternoon (1700–1800 hr).

In experiments in other sections, started at the same time, the majority of larvae had settled by the early afternoon (1400–1500 hr). The lag in settling in these first-mentioned experiments may have been due to initial reluctance of the larvae to settle at such high densities; it is shown later that larvae withheld from suitable settling surfaces for extended periods become less discriminating in their searching behaviour. Presumably larvae which did not find conditions suitable for for settling could swim around and postpone settlement until such time as their searching behaviour and discrimination began to decrease.

It is evident from the results (Table 2) that *S. borealis* is capable of settling and metamorphosing at much higher densities than were observed in natural conditions. Laboratory densities of 64–322 individuals per cm^2 were readily obtained

TABLE 2

EXPERIMENTALLY INDUCED HEAVY SETTLING DENSITIES OF SPIRORBIS BOREALIS ON FUCUS SERRATUS

Expt. No.	No. of Larvae Settling on					*Fucus* Area Available (cm²)	*Fucus* Possible Density per cm²	*Fucus* Actual Density per cm²	Unsettled Larvae*	Total Larvae
	Surface Film	Dish Walls	*Fucus* Upper Surface	*Fucus* Lower Surface	*Fucus* Total					
1	14	2	122	127	249	1·339	222·78	185·96	40	305
2	13	3	62	62	124	0·675	217·78	183·70	7	147
3	16	2	91	58	149	1·378	134·28	108·13	18	185
4	57	0	63	68	131	1·457	133·84	89·91	7	195
5	1	1	51	43	94	1·465	66·89	64·16	2	98
6	46	37	104	100	204	1·195	260·25	170·71	24	311
7	181	2	219	106	235	1·244	428·46	261·25	25	533
8	2	0	112	64	176	1·151	184·17	152·91	34	212
9	127	12	192	182	374	1·128	507·98	331·56	60	573
10	32	10	94	155	249	0·668	291·92	223·05	4	195
11	34	5	72	75	147	1·286	158·63	114·31	18	204
12	64	25	66	53	119	1·313	177·46	90·63	25	233
13	100	55	117	115	232	1·109	408·48	209·20	66	453
14	124	14	163	168	331	1·336	447·61	247·75	129	598
15	24	16	35	28	63	0·944	152·54	66·74	41	144

* Many of these, particularly at the higher densities, had become entangled in mucus but were still alive.

and the larvae showed every indication of metamorphosing normally. Unfortunately suitable food was not available to rear them further. The corresponding range for naturally settled material, which had been especially selected because of its heavy densities (see previous section), was 12–33 individuals per cm^2. It is of interest that although the larvae are probably never forced to settle in natural conditions at densities comparable to those obtained in the laboratory, they can exercise this faculty when the circumstances arise. The tendency for the majority to crowd on the *Fucus*, rather than to occupy the other available surfaces, and in spite of the high population density appearing there, indicated the superior attraction of *Fucus*.

(*c*) *Avoidance of Objects on the Settling Surface*

In describing the gregarious behaviour of setting *S. borealis* larvae, Knight-Jones (1951) observed that "gregariousness soon led to a crowding of from about 10 to 20 recently settled individuals/cm^2 but larvae arriving thereafter sought less crowded areas nearby, on which they spaced themselves out". Experiments in the current series, conducted at the lower of these extremes, lend support to this. Essentially they consisted of placing in each dish a disk of *F. serratus* of upper surface area 0·5 cm^2 on which five small *S. borealis* adults (diameter *c.* 1·0 mm) had been placed to give the critical density (10 per cm^2). Six similar but bare disks were also placed nearby in each dish as alternative settling surfaces. The disks bearing *Spirorbis* are referred to as the treated disks, and the remaining six as the control disks. Larvae were then introduced into each dish and allowed to settle. After 24 hours the numbers of larvae settling and metamorphosing on the upper surfaces of all disks were counted. Since it was difficult to provide disks of identical colour, texture, and "flatness," a considerable degree of replication was made to minimize the effect of these variables, and also of differences in illumination and other factors. Forty-nine dishes, each containing seven disks, were used in each experiment; their arrangement is shown in Figure 5. Preliminary tests showed that the larvae were settling preferentially on the more concave surfaces of each disk. Since flatter disks could not be obtained, all disks were placed with their more concave surface uppermost and the most concave disk was made the treated disk. This made the treated disk slightly more suitable for settlement than the controls, and biased it against the result (see later). A second series of experiments was carried out, in which five round, similar-sized objects were substituted for the *Spirorbis* on the treated disks. These were (1) small beach pebbles, (2) pieces of *Mytilus edulis* L., valve suitably ground down, (3) small empty gastropod shells. These were included to see whether the lower numbers settling on the disks treated with *Spirorbis* adults resulted from a specific interaction, or whether it resulted merely from contact with any raised object on the settling surface. In the results (Table 3) the actual position of the experimental disk during the experiment is given on the left and the disk positions have been rotated the appropriate amount in each case so that the numbers settling on the treated disk appear in the next column. The temperature was 17–19°C and the light dim (17 candles per sq. ft with a Weston meter).

In each of these experiments the total number of larvae settling on the treated disks was lower than the total settling on any one of the control disk series (Table 3).

This was not limited to the treated disks on which *Spirorbis* had been previously placed, but included those bearing similar-sized objects (Table 4). As noted earlier the slightly greater concavity of the treated disks would have tended to encourage settling, when compared with the other disks. Although relatively large numbers of larvae were used, particularly in the substitution experiments, the majority settled and metamorphosed; only about 5 per cent. had not settled after 24 hours. The results can be interpreted as indicating that the larvae were less willing to settle on surfaces already bearing raised objects at a density of 10 per cm^2, than on nearby bare surfaces.

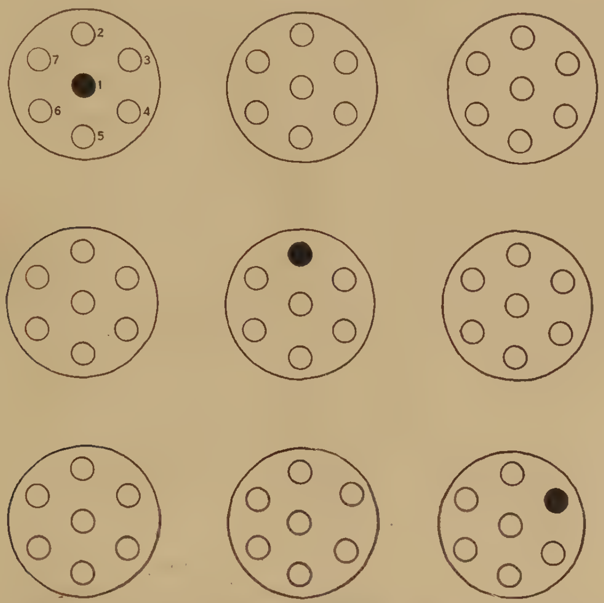

Fig. 5.—Outline of experimental arrangement used in testing reactions of settling *S. borealis* to critically treated *F. serratus* disks. Forty-nine dishes each containing seven *Fucus* disks were arranged in seven rows of seven. Nine of the dishes are shown: ● denotes treated *Fucus* disk bearing five small *S. borealis* adults or similar-shaped objects to give critical density of 10 per cm^2; ○ denotes bare control disks. The treated disk was placed in a different dish in each row and its position, within each dish, was changed in a clockwise direction from position *1* to *7*. Further details in text and Table 3.

IV. DIRECT OBSERVATIONS ON SETTLING BEHAVIOUR

(a) *The Exploratory Movements of Settling Larvae*

Direct observations were made on the reactions of crawling larvae to the presence of grooves or raised objects on the settling surfaces, and on their behaviour after they had been withheld from such surfaces for prolonged periods. Freshly liberated larvae were kept for 4–8 hours in clean beakers of filtered sea-water, which discouraged settlement during this period. They were then transferred to a small dish of filtered sea-water containing a 1·2 cm diameter disk of *F. serratus*, which contained a section of midrib and nearly covered the entire bottom of the dish. Many larvae then alighted on the disk, commenced crawling, and eventually settled

TABLE 3

EXPERIMENTAL SETTLING OF SPIRORBIS BOREALIS ON BARE AND ON TREATED FUCUS SERRATUS SURFACES—FIRST EXPERIMENT

Disk treated by placing five small *S. borealis* adults on it. Experimental arrangement as in Figure 5. Initial density 10 per cm²

Position of Treated Disk	Settlement on							Total Settlement
	Treated Disk	Six Bare Disks in Same Dish						
1	0	1	0	4	0	2	0	7
2	0	0	0	0	1	4	2	7
3	0	1	0	2	7	1	1	12
4	0	2	8	1	0	1	1	13
5	0	1	0	0	0	1	5	7
6	1	5	0	0	2	1	5	14
7	0	7	3	0	1	3	0	14
Totals	1	17	11	7	11	13	14	74

TABLE 4

EXPERIMENTAL SETTLING OF SPIRORBIS BOREALIS ON BARE AND ON TREATED FUCUS SERRATUS SURFACES—SECOND EXPERIMENTAL SERIES

Expt. No.	Treatment	Larvae Settling on 7 Treated Disks (Total Area 3·5 cm²)	Larvae Settling on 42 Control Disks (Total Area 21·0 cm²)	Density per cm²		
				On Treated Disk	On Treated Disk, Corrected*	On Control Disks
I	Five small *S. borealis*, giving initial density of 10 per cm²	1	73	0·3	0·3	3·5
II	As in I	67	1199	19·1	20·6	57·1
III	As in I	13	323	3·7	4·0	15·4
IV	Five gastropod shells	126	1020	36·0	38·9	48·6
V	Five pebbles	125	973	35·7	38·6	46·3
VI	Five pieces of *Mytilus* shell	70	918	20·0	21·6	43·7

* Multiplied by 1·08 to correct for approximately one-thirteenth of surface already taken up by the five small objects on the treated disks.

and metamorphosed, their movements meantime being plotted by means of a camera lucida mounted on a dissecting microscope. The image of the white attachment gland (Fig. 4) was kept as nearly as possible in view under the point of the pencil and it should be noted that the anterior end of the larva was moving about 0·25 mm in front of this point. Consequently, where the settling paths are shown leading towards but apparently turning away just before reaching nearby objects, the larvae did in fact touch them. The temperature was maintained at 18±1°C with a water-bath and the direction of the light incident on the surface is indicated by an arrow in the Figures that follow.

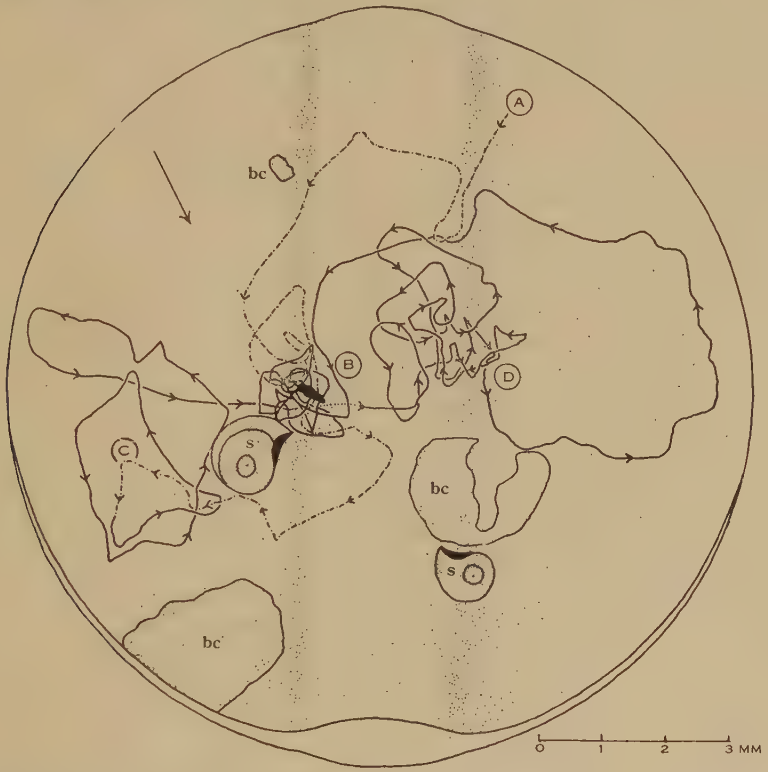

Fig. 6.—Crawling movements of a settling *S. borealis* larva on a *F. serratus* disk containing a section of midrib and previously settled adults of the same species (*s*) and bryozoan colonies (*bc*). The groove areas alongside the midrib have been more extensively traversed than have other parts of the surface. The small arrows indicate the direction the larva was travelling in and the large arrow the direction of the light. Time taken between alighting and settling, 3½ min. Larva about 4 hours old. Details of final settling movements (*B*) in Figure 7. Camera lucida.

There appeared to be basic features of behaviour common to most of these larvae. Providing they were not withheld from the settling surfaces for more than than about 4 hours after liberation, they frequently explored extensively. In such cases the alternating swimming–crawling behaviour described by Knight-Jones (1951) for more recently liberated larvae was scarcely in evidence; the movements consisted mainly of crawling followed by settling. Figure 6 shows the general movements of such a larva over a disk containing a midrib section and several previously settled *S. borealis* and bryozoan colonies, and Figure 7 gives details of its final settling movements. This larva alighted at *A* (Fig. 6), crawled to *B*, and circled twice at *C* before moving on to *D*; crawling was rapid and relatively few turns were made. At *D*, however, the larva began to crawl much more slowly and made frequent turns; the resulting pattern shows that this area was extensively traversed and on several occasions it appeared that the larva was about to settle. Eventually it left this area and crawled rapidly around the periphery of the disk, returning to *B* where it slowed down and made frequent turns. This area was also extensively traversed (Fig. 7) and the larva finally settled as shown. It is notable that the larva made its most intensive exploratory movements in the groove areas (Fig. 6,*B*,*D*) and during its final settling movements touched a nearby adult three times and turned away each time from its edge, finally settling nearly 1·0 mm away (Fig. 7). Many similar cases of larvae tending to explore grooves more thoroughly than other parts of the frond were noted.

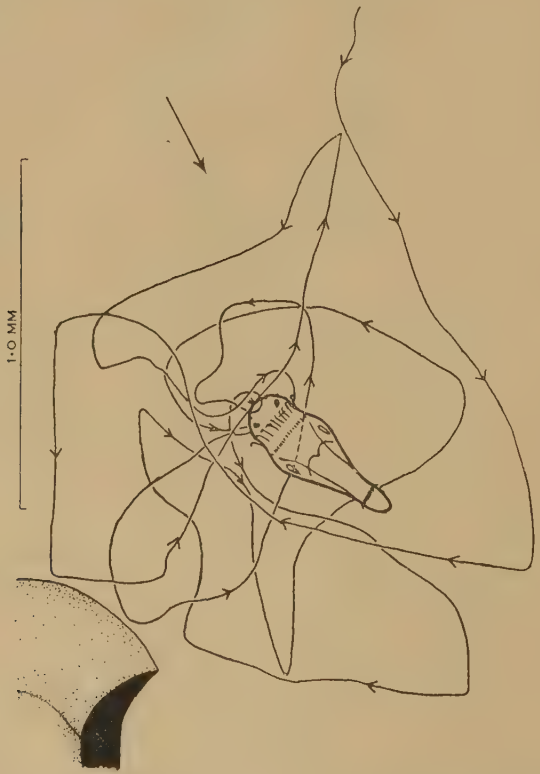

Fig. 7.—Enlargement of area *B* in Figure 6 showing the final settling movements of the larva. Note the avoidance of the nearby adult and the intensive traversing of the area surrounding the settling site. Camera lucida.

Sometimes when a larva encountered a groove shortly after alighting, it remained in or near it until it had settled and did not endeavour to explore other parts of the disk. This was more noticeable in larvae which had been withheld from settling surfaces for about 5–6 hours beforehand. Figure 8 shows an example of this abbreviated settling behaviour. A groove was encountered shortly after alighting and the larva then began to crawl much more slowly. It left the groove on two occasions (*A*,*B*), but returned. There were two excursions in opposite directions along the length of the groove: one of 1·75 mm from the final settling site (*C*) and the other of 1·50 mm (*D*). It seems likely that the larva would have encountered any previously settled individual within these limits, if one had been present. Although the area around the final settling site was intensively traversed over a radius of 1·0 mm there were two "blind spots" (*E*,*F*) where little or no attempts were made.

A large proportion of larvae withheld for longer periods (6–7 hours) settled almost immediately after alighting on the surface, their exploratory movements being similar to those recorded in Figures 9 and 10 and consisting essentially of brief movements close to the alighting points, which in these two examples were on flat parts of the disk surface. The final attachment site of such larvae appeared to be determined by the point at which the larva alighted, rather than the contour of the settling surface. Larvae showing this very abbreviated pattern of behaviour often settled on flat parts of the disks. Both exploratory movements about the final settling site and the reaction avoiding nearby objects were still displayed, but the time taken to settle was shorter and the proportion of larvae that failed to attach was noticeably higher. Finally, when larvae were previously withheld from the settling surfaces for 8 hours or more, much of the settling took place directly on the lighting points. Exploratory movements were restricted to turns within the body length or even to the characteristic 120° lateral swings of the abdomen which immediately precede settlement. These are shown diagrammatically in Figure 11. While there was variation, even between individuals of the same age, there appeared in general to be a steady reduction of the extent of exploratory behaviour as the swimming period was prolonged. The propensity to search widely appeared to be the first to be lost, followed by a disinclination to leave a recently encountered groove on the chance of finding another. Exploratory movements then became restricted to the immediate vicinity of the alighting point, and finally were curtailed to a few turns within the body length (radius *c.* 0·25 mm) or merely to twitching movements of the abdomen. There did not appear to be any relationship between the direction of light and the final orientation of the larvae, as in certain barnacle cyprids (Crisp and Barnes 1954).

(*b*) *Relation between Behaviour and Natural Settlement Pattern*

These observations offer some explanation of the pattern observed in natural populations. Presumably in the populations shown in Plate 1, Figure 1, the majority of larvae encountered the frond early in their free-swimming life since the grooves have been preferentially colonized, as would be expected from the behaviour of larvae less than 5 hours old (Figs. 6–8). Before actually settling many of these larvae may have made exploratory movements up and down the grooves (as in Fig. 8).

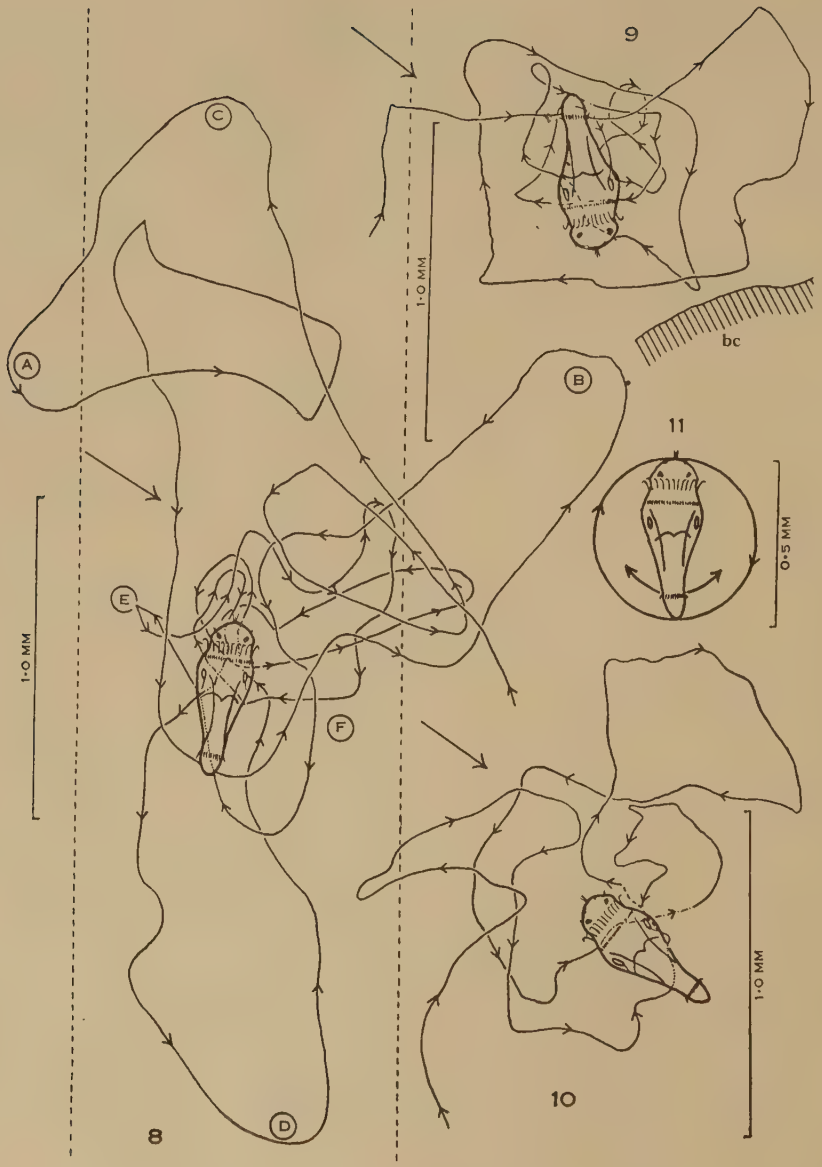

Fig. 8.—Crawling movements of a *S. borealis* larva mainly within a groove (denoted by dotted lines) on *F. serratus*. Larva 5–6 hours old. Time from alighting to settling, 2 min.

Figs. 9 and 10.—Examples of *S. borealis* settling on flat surfaces of *F. serratus* rapidly (1 min) but still showing exploratory movements around the settling sites. Larvae 6–7 hours old. *bc*, Bryozoan colonies.

Fig. 11.—Diagrammatic representation of settling movement of an 8-hour old larva on alighting. Movements were restricted to turns within the body and lateral flexures of the abdomen through a 120° arc. Camera lucida, except for Figure 11.

They avoided settlement near other individuals previously settled in the grooves, since these populations were spaced out about 1–2 mm (Fig. 3). This was probably the result of the final exploratory movements for these have been shown to cover an area of radius about 1–2 mm (Figs. 7–10). A proportion of the larvae alighting on surfaces already occupied at a density of 10 individuals per cm^2 (Table 3) probably swam off again before finally settling; it seems unlikely that they would be able to detect the presence of previously settled individuals before alighting, and they did not settle equally on bare and on previously settled surfaces. Colonization of the flatter parts of the frond after the grooves were occupied would follow as a result of larvae avoiding individuals already established there, or by larvae which had been swimming freely longer (6 or more hours) and were consequently displaying the abbreviated form of searching behaviour (Figs. 9–11). After increasing delay in settling the alighting points and settling sites were gradually coinciding. The overall density per unit area on such fronds did not reach a high value; the maximum settling densities recorded in natural conditions were only 12–13 individuals per cm; but under experimental conditions larvae could settle eventually at 10 times these densities (Table 3). It is suggested that in the sea there is more surface of *F. serratus* in relation to the number of larvae alighting, and in the forced conditions of the laboratory they delayed settling until they reached the stage where the abbreviated behaviour of settling appeared.

The length of time the larvae have been free-swimming, and the distribution and density of previously settled individuals or the presence of similar-sized raised objects on the surface of the frond, would appear to be significant factors in determining the ultimate pattern of settlement. The behaviour mechanisms ensure that, as far as possible, the adult is afforded sufficient territory to reach maturity (*c.* 2·0 mm diameter) without interference on the appropriate substrate, but it is interesting to note that the behaviour is modified in the course of time. The exploratory behaviour can be considerably abbreviated. This is in accordance with many other instinctive reactions where the ultimate goal overrides secondarily imposed discrimination activity (Thorpe 1948).

(*c*) *Initial Attachment of the Larva*

Knight-Jones (1951) has already described the attachment and metamorphosis of *S. borealis* and it is not proposed to enter into this in greater detail except for the initial stages of attachment; these take place during the first few minutes of the process. The first indication that attachment is about to take place occurs after the larva has become motionless (except for twitchings of the abdomen) on the settling site. The attachment gland on the dorsal surface of the abdomen then gives a series of powerful muscular contractions which force out a white secretion from the posterior part of the gland and over the posterior half of the larvae; the secretion flows down over the sides of the larva forming and largely enclosing it in a tube which is closed at the posterior end. The material gradually becomes semitransparent and adheres where it comes in contact with the substrate. It is also elastic, for it bulges out when the larval chaetae press out against it, but returns to its original close-fitting sheath when they are withdrawn. After the formation of this primary tube, the larva is not readily dislodged from the substrate either by a sharp jet of sea-water from a pipette or by a jab from a needle. It soon rolls over, so that the dorsal surface is against the substrate. The collar retracts towards the head but returns shortly afterwards, gripping the outside surface of the attachment tube as it does so. This method of attachment ensures that the larva is not readily dislodged from its attachment site during the first few minutes when it is changing from a crawling larva to a fixed young worm. The rapid formation of the elastic attachment tube secures an immediate bond with the substrate and enables the larva to use its chaetae, uncini, and collar to retain itself with the tube while its anterior end is undergoing cataclysmic metamorphosis and developing the operculum, branchial crown, and other structures characteristic of the young worm.

V. Acknowledgments

Thanks are due to the Director of the Marine Biological Station, Dr. D. J. Crisp, for extending facilities, supervising the research, and for his interest and encouraging help during it. This work forms part of a programme on the biology of fouling organisms carried out in cooperation with the Royal Australian Navy.

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SETTLING OF SPIRORBIS BOREALIS

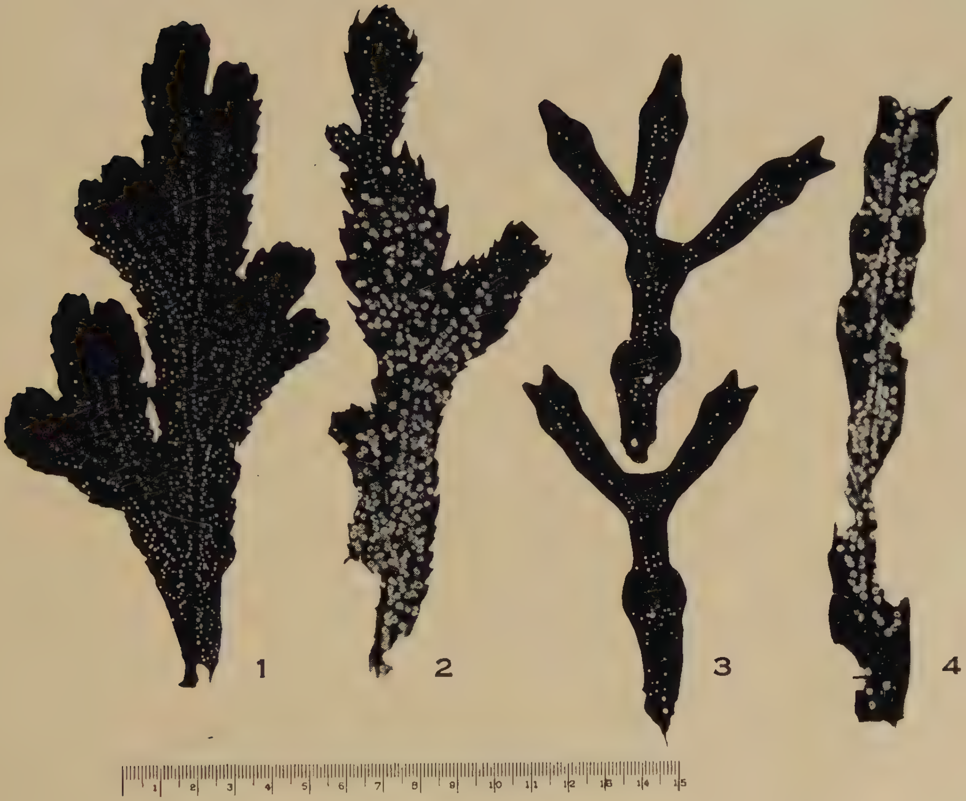

Fig. 1.—Newly settled *S. borealis* on *F. serratus* showing outlining of midrib due to settlement in the grooves parallel and alongside it. Scale in cm.

Fig. 2.—Older *S. borealis* on *F. serratus*. The outlining of the midrib is less distinct and there is increased settlement on other parts of the frond.

Fig. 3.—Newly settled *S. borealis* on *F. vesiculosus* fronds showing similar settlement alongside the midrib, and around the bases of the globular bladders.

Fig. 4.—Older *S. borealis* on *F. vesiculosus* showing the arrangement more clearly.

THE AUSTRALIAN PORTUNIDS (CRUSTACEA: PORTUNIDAE)

IV. REMAINING GENERA

By W. Stephenson* and B. Campbell*

[*Manuscript received August* 7, 1959]

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Summary

Keys to the Indo-Pacific subfamilies, genera, and species are given. Subfamily names are discussed, Portuninae being used in a new sense and Macropipinae being proposed for Alcock's Portuninae.

Catoptrus and *Aeneacancer* are synonymized with *Libystes* and *Ovalipes* respectively so that 11 genera (*Carcinus*, *Nectocarcinus*, *Libystes*, *Carupa*, *Ovalipes*, *Macropipus*, *Lissocarcinus*, *Caphyra*, *Lupocyclus*, *Scylla*, and *Podophthalmus*) containing 17 species are recorded from Australia, including two new species. Whole specimens, male abdomens, and male pleopods of these are illustrated and full descriptions are given in selected cases.

I. Introduction

Previous papers of this series have dealt with the three genera which are most abundantly represented in the Australian collections, viz. *Thalamita* Latreille (Stephenson and Hudson 1957), *Charybdis* de Haan (Stephenson, Hudson, and Campbell 1957), and *Portunus* Weber (Stephenson and Campbell 1959). Because many species of these genera are found in Australia and because the first pleopods of the males had rarely been described adequately or figured, these genera were treated fairly fully. Comparison of first male pleopods served to indicate species groups, and in most cases these confirmed groupings within the genera which had been suggested previously on the basis of general facies.

The remaining genera are spread between all the subfamilies, with relatively few Australian species in each. Because the literature is scattered it has been thought

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desirable to consolidate the essentials into one paper, and in particular to include relevant keys to and figures of the intact animals. Some genera and species have been treated adequately in recent literature, and in these cases the synonymy is greatly abbreviated. In cases where changes are proposed a fuller synonymy is given. With two exceptions all species have been described previously and hence, in general, specific diagnoses rather than descriptions are given. Detailed treatment has been reserved for (i) structures not previously described in sufficient detail, especially first pleopods of males and (ii) cases where consideration of the present specimens leads to alterations of published descriptions.

Descriptions of first pleopods of males, unless otherwise stated, refer to unflattened appendages as viewed from the ventral surface with abdomen uplifted. All figures are of the left pleopods, i.e. right as viewed from the under surface of the crab. It should be noted that the concave border lies to the outside of the animal and the convex towards the inside. In some cases permanent balsam mounts were made, after treating with caustic potash and staining in fast green; in other cases temporary mounts were made in glycerol and alcohol. All figures of pleopods are either based upon camera lucida outlines or were drawn with the assistance of a squared micrometer eyepiece.

The ultimate branches of the keys terminate in three different types of references: (i) with only an author and date: in such cases the entity which has been keyed out is treated in later pages of the present paper; (ii) with author, date, and pagination: here the keyed-out entity has been treated in a previous paper of the present series; and (iii) with author, date, pagination, and the words "not recorded from Australia".

II. The Family

H. Milne Edwards (1834, p. 432) referred to "Tribu des Portuniens", and Dana (1852*b*, pp. 267, 290) first used the term "Portunidae". He used it in a more restricted sense than at present, and its present use dates from Miers (1886, p. 169). The early synonymy of the family is given in Alcock (1899, p. 5).

Diagnostic features are given by Alcock (1899, pp. 5–7), Borradaile (1907, p. 481), Sakai (1939, pp. 365–6), and Barnard (1950, pp. 139–40). The obvious features of typical portunids are the flattened fifth pair of legs and the structure of the carapace.

The fifth legs as a whole are usually flattened, especially the last two joints, and this has been assumed to be an adaptation for swimming. While these legs are used for swimming in the genus *Portunus*, many of the so-called swimming crabs do not swim at all frequently or convincingly. Many species use them for excavation and even *Portunus pelagicus* uses them occasionally for this purpose.

It has been suggested previously (Stephenson, Hudson, and Campbell 1957; Stephenson and Campbell 1959) that the more active swimmers and burrowers may be later evolutionary developments in the family, in which case genera such as *Carcinus* Leach, *Nectocarcinus* A. Milne Edwards, and *Libystes* A. Milne Edwards, without the typical flattened appendages, could be regarded as primitive. *Caphyra*

Guérin, also without flattened appendages, is probably specialized but in a manner different from the majority of the family.

The carapace is usually wider than long, depressed or slightly convex, and is rarely areolated. The front is usually broad and cut into teeth. The flat, broad (and pointed) carapace may well be a form of streamlining related to lateral swimming (Stephenson and Campbell 1959) and again the forms with the more convex, narrower, and "squarer" carapaces could be regarded as primitive (e.g. *Carcinus*, *Nectocarcinus*, *Libystes*) or specialized for a different mode of life (e.g. *Caphyra*).

The following less conspicuous characters have diagnostic value at the family level: orbits complete, no rostrum, first antenna folding slantwise or transversely, carpus of third maxilliped articulating at or near the antero-internal angle of the merus, usually a small lobe on the inner angle of the endopodite of the first maxilliped, male opening coxal.

The portunids as a whole are close to the cancrids and xanthids, and separation of genera such as *Carcinus* from the xanthids is difficult and somewhat arbitrary. As Alcock has noted (1899, p. 4) "The Carcininae by way of *Carcinus*, approach the Xanthidae by way of *Hoploxanthus*".

III. The Subfamilies

Sakai (1939) recognized six subfamilies, viz.: Carcininae Alcock, 1899; Catoptrinae Borradaile, 1907; Portuninae Alcock, 1899; Caphyrinae Alcock, 1899; Lupinae Alcock, 1899; and Podophthalminae Borradaile, 1907 (attributed by Sakai to Rathbun 1930). Edmondson (1954) recognized the same subfamilies but used Caphrinae for the Caphyrinae. These appear the most natural groupings yet suggested and differ from Alcock's four original subfamilies by recognizing the separateness of Borradaile's Catoptrinae and Podophthalminae although not accepting his Portuninae or Carupinae. Rathbun's (1930) concept of the subfamilies was evidently similar to Sakai's, allowing for her work being restricted to the American genera and for some changing of names.

If it is accepted that there are six subfamilies, their naming is a matter of difficulty. Following upon resolutions of the International Commission on Zoological Nomenclature (1955) *Carcinides* Rathbun has been suppressed in favour of *Carcinus* Leach, so Alcock's Carcininae stands in favour of Rathbun's Carcinidinae.

As will apear later in this paper the genus *Catoptrus* Milne Edwards is a synonym of *Libystes* Milne Edwards. Since it is a junior subjective synonym the subfamily name Catoptrinae can remain unchanged (Add. Règles Internat. 1953, item 54, p. 36).

Alcock's Portuninae is based on *Portunus* Fabricius, 1798, which is a junior homonym of *Portunus* Weber, 1795 (see Internat. Comm. Zool. Nom. 1956). Of the later synonyms of *Portunus* Fabricius, *Macropipus* Prestandrea, 1833, has priority over *Liocarcinus* Stimpson & Pourtalès, 1870. Hence the Portuninae Alcock must become Macropipinae (nom. nov.).

The genus *Lupa* Leach has been rejected officially for *Portunus* Weber (Internat. Comm. Zool. Nom. 1956) and Alcock's Lupinae should therefore be replaced. The subfamily name Portuninae, containing the genus *Portunus*, must be applied here instead of Borradaile's Thalamitinae. This concept of the *Portuninae* is quite different from that of Alcock and others.

The subfamily names Caphyrinae Alcock and Podophthalminae Borradaile remain unaltered.

The features of these subfamilies are:

(i) *Carcininae.*—Legs stout and long, at least one pair as long as chelipeds, last pair with lanceolate dactylus but otherwise similar to the 3 other pairs. Carapace not broad, anterolateral borders cut into 4 or 5 teeth. Basal joint of second antenna fixed, longer than broad, lying in longitudinal axis of carapace.

(ii) *Catoptrinae.*—Last pair of legs either lanceolate or paddle-shaped. Carapace transversely elliptical and convex in both directions, anterolateral borders either toothed or entire. Basal joint of second antenna long and oblique, flagellum standing in orbital hiatus.

(iii) *Macropipinae.*—Legs stout and long, last pair typical paddles. Carapace not very broad, 5 anterolateral teeth. Second antenna arising from orbital hiatus, and lying almost in the longitudinal axis of the carapace, flagellum standing inside the orbit.

(iv) *Caphyrinae.*—Legs short, last pair either claw-shaped or lanceolate. Carapace not very broad, 4 or 5 anterolateral teeth. Basal joint of second antenna with its antero-external angle lobulate, the flagellum excluded from the orbit.

(v) *Portuninae.*—Legs shorter than chelipeds, last pair typical paddles. Carapace typically broad to very broad, 4–9 anterolateral teeth. Basal joint of second antenna usually broad, antero-external angle sometimes lobulated, flagellum sometimes included in the orbit.

(vi) *Podophthalminae.*—Eye stalks very long, orbits occupying whole anterior border of carapace except for the narrow front. Few anterolateral teeth. Last legs paddle-shaped. Basal joint of second antenna short, flagellum included in the orbit.

The subfamilies can be keyed as follows:

1. Eyestalks enormously long .... PODOPHTHALMINAE Borradaile (1907)
Eyestalks normal 2

2(1). Carapace broad (transversely elliptical) and convex in both directions. (Antennal flagellum in orbital hiatus) .... CATOPTRINAE Borradaile (1907)
If carapace broad, not convex in both directions 3

3(2). Chelipeds and legs both long, chelipeds longer than all legs, carapace typically broad .... PORTUNINAE, usus nov.
Chelipeds and legs both long, one pair of legs as long as chelipeds, carapace relatively narrow 4
Chelipeds and legs both short, carapace relatively narrow .. CAPHYRINAE Alcock (1899)

4(3). Last legs typically not noteworthily different from other pairs, basal joint of second antenna narrow .... CARCININAE Alcock (1899)
Last legs typical swimming paddles, basal joint of second antenna broad ....
.... MACROPIPINAE, nom. nov.

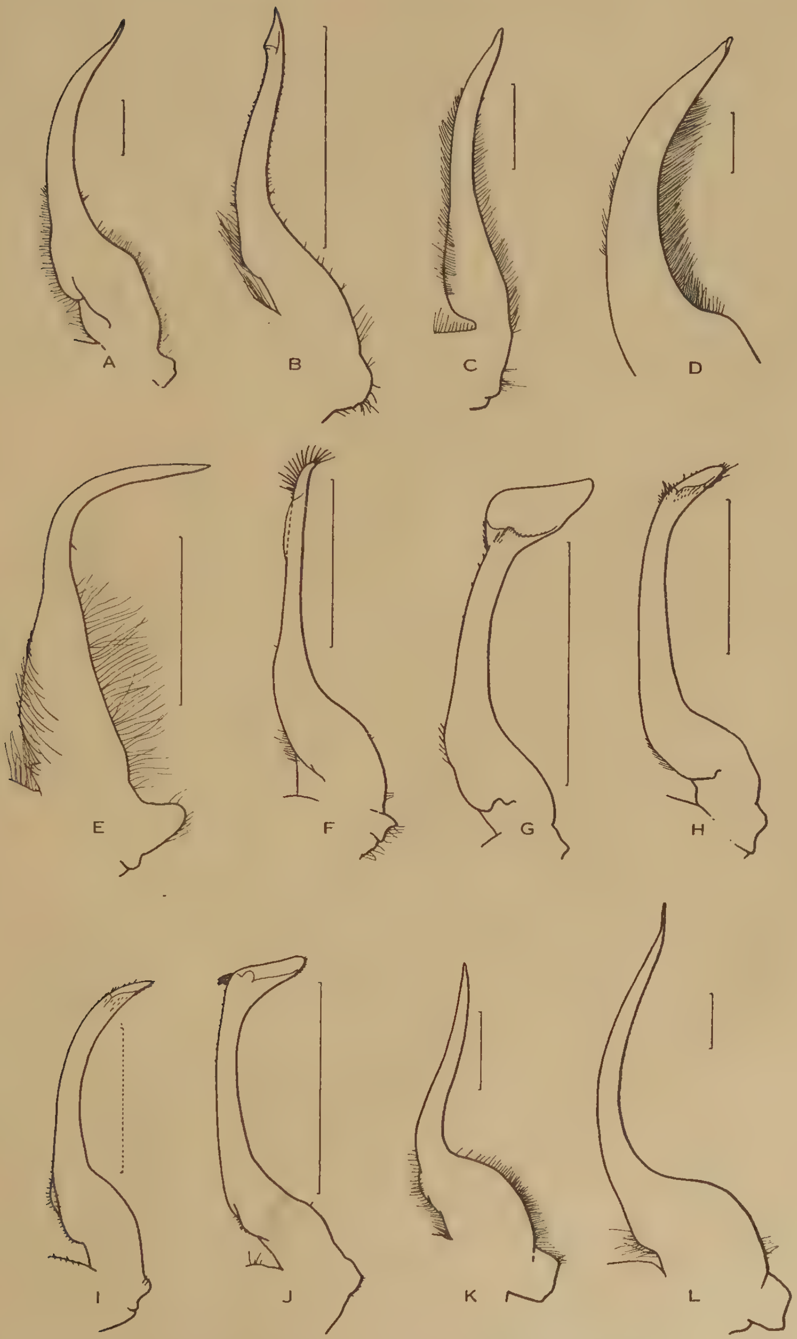

Fig. 1.—Left first male pleopods. Scale lines 2 mm unless otherwise stated. *A*, *Carcinus maenas*; *B*, *Libystes paucidentatus*; *C*, *Ovalipes punctatus* (right pleopod reversed); *D*, *O. molleri* (right pleopod reversed); *E*, *Macropipus corrugatus* (right pleopod reversed); *F*, *Lissocarcinus polybioides* (right pleopod reversed); *G*, *Caphyra laevis*; *H*, *C. rotundifrons*; *I*, *C. yookadai* (right pleopod reversed, scale line 1 mm); *J*, *C. fulva*; *K*, *Lupocyclus rotundatus*; *L*, *Podophthalmus vigil*.

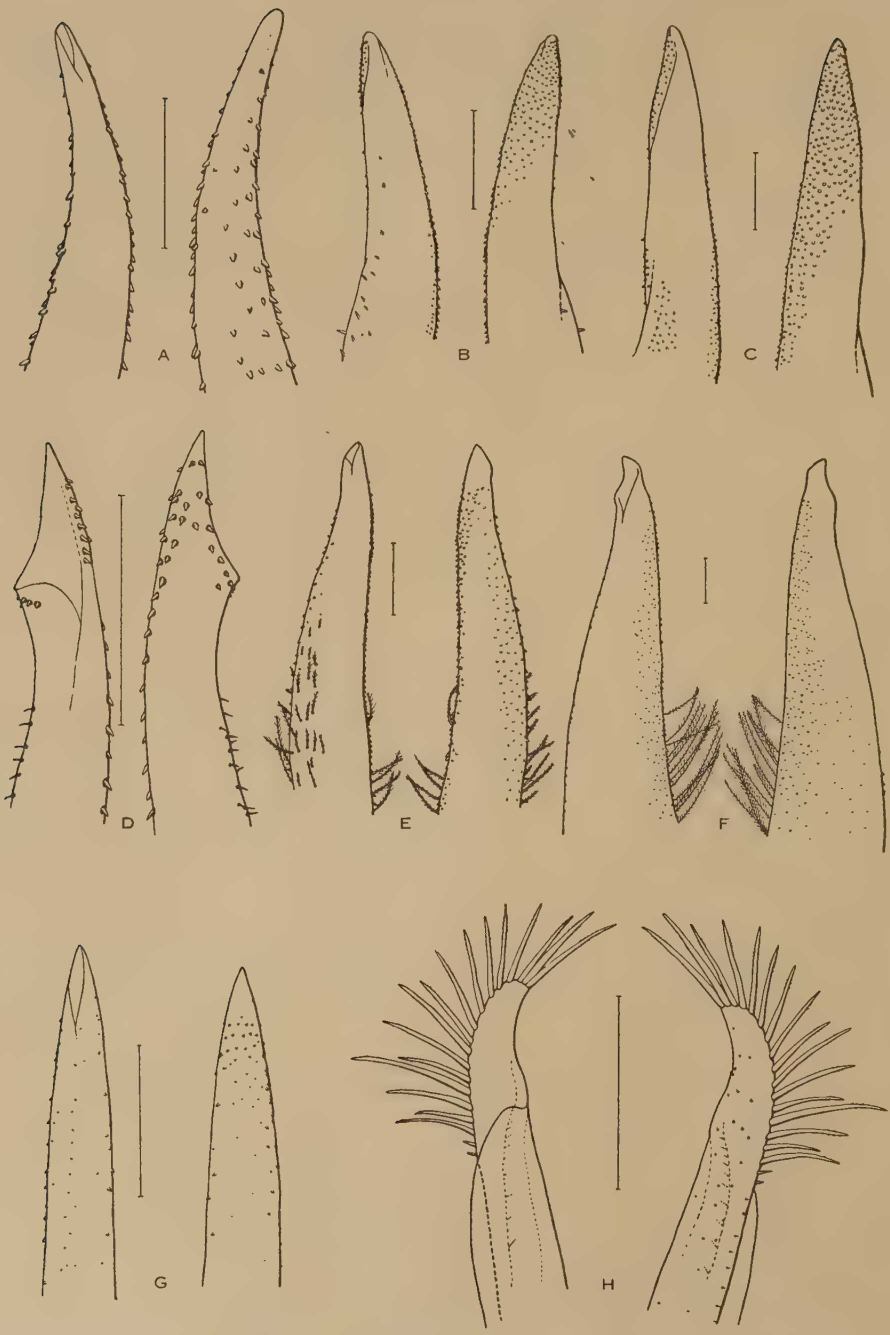

Fig. 2.—Tips of left first male pleopods. The upper surfaces are to the left of the scale lines, the under surfaces to the right. Scale lines 0·5 mm. *A*, *Carcinus maenas*; *B*, *Nectocarcinus integrifrons* (right pleopod reversed); *C*, *N. tuberculosus* (right pleopod reversed); *D*, *Libystes paucidentatus*; *E*, *Ovalipes punctatus* (right pleopod reversed); *F*, *O. molleri* (right pleopod reversed); *G*, *Macropipus corrugatus* (right pleopod reversed); *H*, *Lissocarcinus polybioides* (right pleopod reversed).

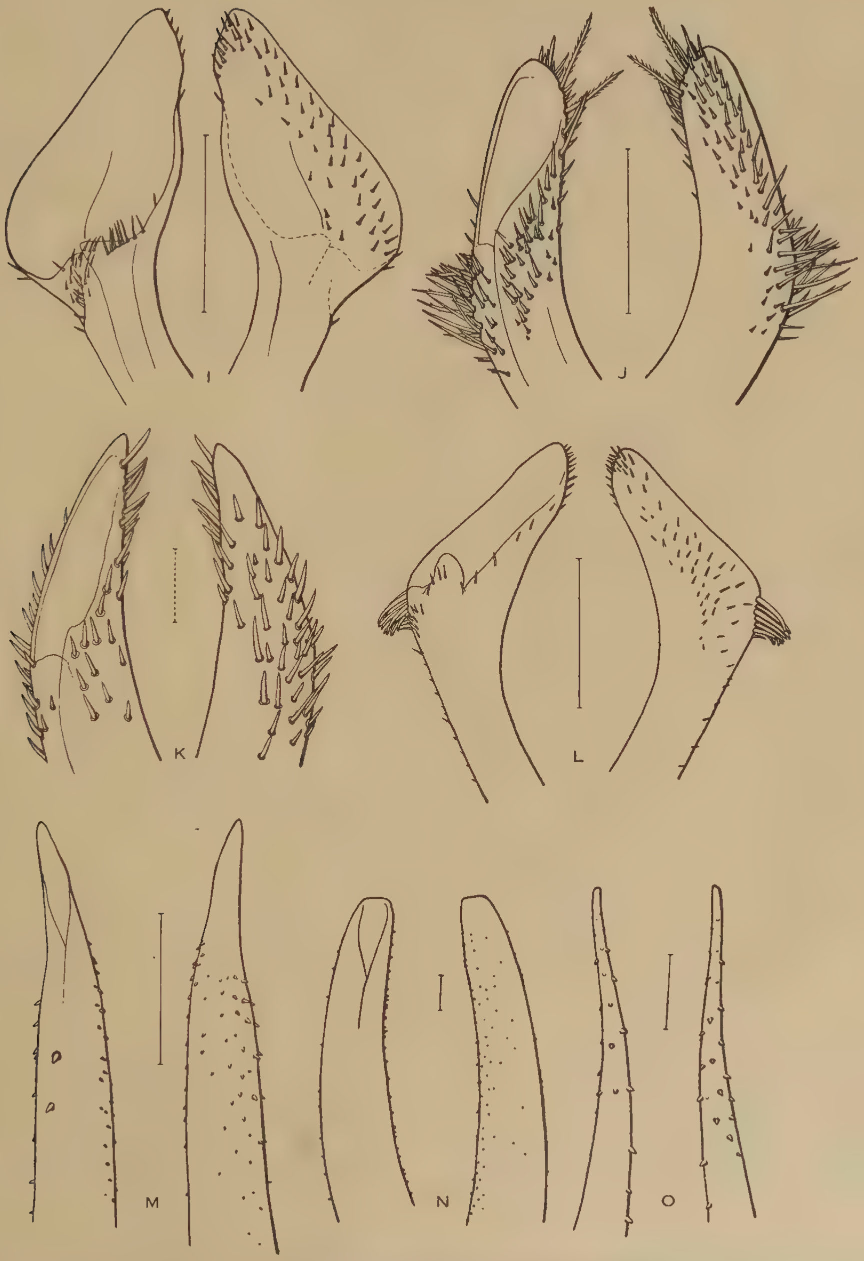

Fig. 2 (*continued*).—Tips of left first male pleopods. The upper surfaces are to the left of the scale lines, the under surfaces to the right. Scale lines 0·5 mm unless otherwise stated. *I*, *Caphyra laevis*; *J*, *C. rotundifrons*; *K*, *C. yookadai* (right pleopod reversed, scale line 0·1 mm); *L*, *C. fulva*; *M*, *Lupocyclus rotundatus*; *N*, *Scylla serrata*; *O*, *Podophthalmus vigil*.

IV. DESCRIPTION OF GENERA AND SPECIES IN THE DIFFERENT SUBFAMILIES

Subfamily **CARCININAE** Alcock, 1899

KEY TO INDO-WEST-PACIFIC GENERA OF SUBFAMILY CARCININAE

1. 4 anterolateral teeth .... *Nectocarcinus* A. Milne Edwards (1860)
5 anterolateral teeth 2

2(1). Last pair of legs swimming paddles .... *Portumnus* Leach (1814, p. 430) (not recorded from Australia)
Last pair of legs not swimming paddles .... *Carcinus* Leach (1814)

Genus CARCINUS Leach

Carcinus Leach, 1814, pp. 390, 429. Alcock, 1899, p. 12 (early synon.). Internat. Comm. Zool. Nom., 1955, pp. 321–38.

Carcinides Rathbun, 1897, p. 164; 1930, p. 14.

CARCINUS MAENAS (L.)

Figs. 1*A*, 2*A*; Plate 1, Fig. 1; Plate 5*A*

Cancer maenas L., 1758, p. 627.

Carcinus maenas (L.). Leach, 1814, p. 429. Alcock, 1899, pp. 13–14 (early synon.).

Carcinus mediterraneus Czerniavsky, 1884, p. 177. Holthuis and Gottlieb, 1958, pp. 82–5.

Carcinides maenas (L.). Rathbun 1897, p. 164; 1930, pp. 15–18, fig. 4 (synon.). McNeill, 1953, pp. 92–3.

Material Examined

NEW SOUTH WALES: At Macleay Museum: ♂ 17 mm, "Sydney" (locality suspect). VICTORIA: At Australian Museum: ♂ 58 mm, ♀ 37 mm, Queenscliffe (Reg. No. G5458). ♀ 41 mm, ♀ 65 mm Bastion Point, near Mallacoota, Misses E. Pope and I. Bennett (Reg. No. P12679–80, see McNeill 1953). At National Museum, Victoria: 3 ♂♂ 43, 47 (figured), 67 mm; 4 ♀♀ 37–52 mm, on sandbank among *Zostera*, Rosebud, 6.xii.58, Miss J. Hope McPherson (no Reg. No.).

Recorded habitats.—Rock crevices high on beach.

Description

General.—Adequately described both generically and specifically by Alcock (1899) and Rathbun (1930) *inter al.* It is readily identifiable by the keys and general facies.

Male pleopod.—Rather long, curved, with the neck tapering evenly to a fine curved tip. Beyond the basal lobes on both outer and inner surfaces long bipinnate hairs are visible for a short distance. These are followed on the outer side by a band of short stout spinules which extend to the tip. The proximal members of this band are broad and blunt becoming smaller, sharper, and backwardly directed as one moves to the tip. Stout, backwardly directed spinules are present on the distal quarter of the inner side, extending to the under surface to give a sparse covering for a short distance back from the tip.

Comments

Holthuis and Gottlieb (1958) have resurrected the species *C. mediterraneus* Czerniavsky, 1884, citing the opinions of Drs. Isabella Gordon, R. Zariequiey,

J. Forest, and L. B. Holthuis that there are constant differences between the Atlantic and Mediterranean specimens (Forest 1957). Holthuis and Gottlieb mention such differences in the shape and granulation of the carapace and also in the pleopods but do not describe them, nor are they given by Forest (1957). The only description of the features characterizing the Mediterranean form are given by Demeusey and Veillet (1953) and summarize as follows: thicker carapace, carapace regions more distinct and more rugose, last anterolateral tooth pointing obliquely, shorter antennular articles, internal flagellum generally with 3 articles excluding the terminal one as against 4 or 5, antennae longer and with more articles, basal article carrying teeth on lateral external border but the ventral face of the lateral external border smooth (vice versa in Atlantic specimens), chelae with accentuated carinae and markedly pilose carpopodite, female abdomen much broader.

The present specimens resemble the American one figured by Rathbun (1930, fig. 4) as regards distinctness of carapace regions and shape of anterolateral teeth. They resemble the Mediterranean ones in having 5 articles on the antennule and in having small teeth on the lateral external border of the basal antennal joint. The chelae are not markedly carinate nor is the carpopodite pilose.

It would appear that specimens from many areas should be examined in detail before the Mediterranean form could be given specific status. It would be especially helpful if the details of pleopod structure mentioned by Holthuis and Gottlieb could be figured and described in detail.

It should also be noted that Demeusey and Veillet were able to cross the Atlantic and Mediterranean forms and obtain viable eggs.

Distribution

North Sea almost to the Arctic, Baltic, Atlantic coast of North America, Brazil, Black Sea, Bay of Panama (Alcock 1899).

Very doubtfully from Hawaii (Edmondson 1954) and from the Red Sea (Monod 1938).

Australian records are: Australia but doubtful (Alcock 1899); Frankston to Port Arlington near Port Phillip, Victoria (Fulton and Grant 1900); Port Phillip, Beaumaris and elsewhere, Port Melbourne (Ward 1929); Mallacoota Inlet, Victoria (McNeill 1953); Port Phillip (Edmondson 1954).

When this species was recorded at Port Phillip by Fulton and Grant (1900) it was described as "plentifully distributed" and considered an introduced species. McNeill (1953) supported this view, and in recording it from a locality 400 miles distant from Port Phillip, firmly believed that the species had spread since 1900. It should be borne in mind that our general knowledge of portunid distributions in Victoria is fragmentary. A more detailed knowledge of the Australian distribution of *Carcinus* at the present time is desirable.

It should be noted that European workers (e.g. Palmer 1927) regard the widespread distribution of *Carcinus* as a natural phenomenon and in harmony with the presence of primitive portunid features. Demeusey and Veillet (1953) suggest it may be a widespread survivor of the Sea of Tethys.

The species is abundant on the cooler North Atlantic coasts of America and Europe and occupies the crevices and under-stone habitat which in lower latitudes house grapsids and xanthids.

It shows primitive features relating it to the xanthids and cancroids, and can possibly be regarded as an isolated offshoot from near the base of the portunids. The main evolution of the family has evidently occurred in warmer waters with the possibility of "relics" remaining in higher latitudes. This concept is supported by the fact that the nearest living genus, viz. *Nectocarcinus*, is restricted to the cooler waters of the Southern Hemisphere.

Genus NECTOCARCINUS A. Milne Edwards

Nectocarcinus Milne Edwards, A., 1860, pp. 219–20; 1861, p. 404. Haswell, 1882*b*, p. 81.

Generic Description (after A. Milne Edwards 1861, pp. 406–7).

Carapace.—Thick, neither very wide nor very convex, regions well defined. Anterolateral borders with the front forming a regular curve of short radius, whose centre lies in the anterior part of the cardiac region. Front protruding, either entire or subdivided.

Anterolateral teeth.—Four, of which the first is the broadest and the last small and sharp.

Basal antennal joint.—Broad, narrow, fused to the front.

Third maxilliped.—Elongate, third article hollowed on outer surface.

Cheliped.—Short and robust.

Walking legs.—Robust and laterally compressed.

Fifth leg.—Not adapted for swimming but wider than in *Carcinus*; propodus broadened, dactyl lanceolate except in *N. antarcticus* (Jacquinot & Lucas, 1853, fide Hodgson 1902; and Richardson 1949, pl. 1, fig. 1*a*).

The genus is not truly Indo-West-Pacific, as Balss (1935) has noted, but is restricted to Australia, New Zealand, and South America. Apart from the two Australian species, *N. antarcticus* occurs in New Zealand and Chatham I. while *N. bullatus* Balss, 1924, is found at Juan Fernandez.

Distinctions between Australian Species

The two Australian species (*integrifrons* and *tuberculosus*) have somewhat similar distributions and habitat and younger specimens of the two species can easily be confused. The front in *N. integrifrons* is finely granular and rounded, with the median notch minute or absent, whereas in *N. tuberculosus* the front is more coarsely granular and the median notch is always distinct. The shape of the male pleopod also provides a clear distinction between younger specimens, being evenly tapered throughout its length in *N. integrifrons* while in *N. tuberculosus* there is a more distinct separation into basal area and neck. Larger specimens of *N. tuberculosus* differ markedly from smaller specimens and also from *N. integrifrons* in having: (1) prominent spiniform granules on the front, anterior part of carapace, and upper surfaces of hands and wrists; (2) rounded, rather than crested anterolateral borders, and (3) the highest part of the carapace apparently further forward, and the posterior half less convex from side to side.

The difficulties in distinguishing these sibling species are such that the key which follows is only workable on the largest specimens, with a carapace width greater than 70 mm.

KEY TO THE KNOWN SPECIES OF GENUS NECTOCARCINUS

1. Front (excluding inner orbital angles) 4-lobed 2
Front with 2 broad lobes separated by a small but distinct notch (older specimens with spiniform tubercles on front of carapace) . . *N. tuberculosus* (A. Milne Edwards) (1861)
Front entire, rarely with a minute notch ....*N. integrifrons* (Latreille) (1825)

2(1). Anterolateral teeth broad and blunt, becoming smaller and sharper posteriorly ......
N. antarcticus (Jacquinot & Lucas) (1853, p. 51, pl. v, fig. 4) (not recorded from Australia)
Anterolateral teeth all sharp and subequal ....
............*N. bullatus* Balss (1924, pp. 335–6, fig. 2) (not recorded from Australia)

NECTOCARCINUS INTEGRIFRONS (Latreille)

Fig. 2*B*; Plate 1, Fig. 2; Plates 5*B*, 6*A*

Portunus integrifrons Latreille, 1825, p. 192. Milne Edwards, H., 1834, p. 445. Kinahan, 1858, pp. 120–1.

Nectocarcinus melanodactylus Milne Edwards, A., 1860, p. 220.

Nectocarcinus integrifrons (Latreille). Milne Edwards, A., 1860, p. 220; 1861, pp. 406–7, pl. xxxviii. Hess, 1865, p. 139. Miers, 1874, p. 2, pl. 1, fig. 3; 1876, p. 30. Haswell, 1882*b*, pp. 81–2 (synon.). Miers, 1884, p. 234. Fulton and Grant, 1906, p. 18. Rathbun, 1923, p. 130. Hale, 1927, pp. 152–3, fig. 153. Chilton and Bennett, 1929, p. 753. Ward, 1929, p. 79, fig. iv. Balss, 1935, p. 130.

Material Examined

42 ♂♂ (8–80 mm); 49 ♀♀ (10–70 mm). One ovigerous ♀ from month of March.

NEW SOUTH WALES: Port Stephens, Port Jackson, Jervis Bay, Port Hacking. VICTORIA: Port Phillip. TASMANIA: Derwent R. SOUTH AUSTRALIA: Kangaroo I.

Recorded habitats.—Intertidal, dredged 2–7 fm.

Material illustrated.—Plate 1, Figure 2: ♂ 65 mm, South Australia (S. Aust. Mus. Reg. No. C1247). Male pleopod: 36 mm, Kangaroo I., pres. June 1920, E. Troughton (Aust. Mus. Reg. No. P4823).

Description

General.—Considered unnecessary.

Male pleopod.—Moderately stout without marked lateral curvatures. The appendage is twisted in a corkscrew fashion which makes recognition of the normal bands of spinules difficult. These spinules are short and blunt and the main band begins on the upper outer surface, curves to the under surface, and reappears subterminally on the inner surface at the tip. Just beyond the basal lobes the upper surface is concave for a small area and the outer edge is relatively smoothly curved.

Distribution

Recorded only from Australia and New Zealand (Miers 1876; Chilton and Bennett 1929). Within Australia from Port Jackson (Haswell 1882*b*; Miers 1884), Tasmania (Miers 1876; Haswell 1882*b*; Guiler 1952), Port Phillip (Kinahan 1858; Ward 1929) and Fremantle (Balss 1935).

Miers (1884) records this species from Port Curtis (Queensland) but because of its isolation this record is highly suspect.

NECTOCARCINUS TUBERCULOSUS A. Milne Edwards

Fig. 2*C*; Plate 1, Fig. 3; Plates 5*C*, 6*B*.

Nectocarcinus tuberculosus Milne Edwards, A., 1860, p. 220; 1861, pp. 405–6, pl. xxxvii. Miers, 1874, p. 2. Haswell, 1882*b*, p. 82. Hale, 1927, p. 153, fig. 154.

Material Examined

15 ♂♂ (13–90 mm); 9 ♀♀ (11–85 mm). Ovigerous ♀♀ from month of August; smallest ovigerous ♀ 25 mm.

NEW SOUTH WALES: Port Jackson, Eden. VICTORIA: Port Phillip, Beaumaris. TASMANIA: King I., Wedge Bay, Derwent R., Hobart, Simpson's Bay, Catamaran, Recherche Bay, Tasman I. off Cape Pillar, Bay of Fires.

Material Illustrated.—♂ 33 mm, Simpson's Bay, Derwent R., pres. Aug. 1926, M. Ward (Aust. Mus. Reg. No. P8653).

Description

General.—Considered unnecessary.

Male pleopod.—Very similar to *N. integrifrons* except that (1) the appendage is relatively thinner, particularly in the subterminal region; (2) the concavity of the upper surface just beyond the basal lobes is extensive and obvious; (3) there is a marked convexity of the lateral external border in this region.

There are minor differences in spinulation between the limited number of juvenile specimens whose pleopods have been examined but these differences are hard to see and do not always seem to apply to the larger specimens where there is a risk of spinules having been lost.

Distribution

From Victoria (Ward 1929) and Tasmania (A. Milne Edwards 1861; Haswell 1882*b*; Rathbun 1923; Guiler 1952).

Subfamily **CATOPTRINAE** Borradaile, 1907

The genera contained in this subfamily were originally placed by Alcock (1899, 1900) in two different families, *Carupa* Dana being placed in the Portunidae and *Catoptrus* and *Libystes* in the Gonoplacidae (=Goneplacidae). Tesch (1918) retained *Catoptrus* and *Libystes* in the latter family but most recent authors, for example Sakai (1939) and Edmondson (1954), have followed Borradaile in keeping the three genera together as a subfamily of the Portunidae. The resemblance to the subfamily of the Pseudorhombilinae Alcock, 1900, of the Goneplacidae, and especially to such genera as *Carcinoplax* H. Milne Edwards, 1852, is however extremely close. It seems probable, therefore, that the family Portunidae is a diphyletic group, with one branch stemming from a *Carcinus*-like form and the second from a *Carcinoplax*-like form. If so this would be an interesting case of parallel evolution, and would also call for the creation of a new family.

KEY TO INDO-WEST-PACIFIC GENERA OF SUBFAMILY CATOPTRINAE

Anterolateral border of carapace entire or bearing at most 6 teeth; arm and wrist of cheliped usually unarmed .... *Libystes* A. Milne Edwards (1867)

7 anterolateral teeth (sixth the largest); arm and wrist of chelipeds bearing teeth .... *Carupa* Dana (1851)

Genus LIBYSTES A. Milne Edwards

Libystes Milne Edwards, A., 1867, p. 285; 1868, p. 83. Alcock, 1900, pp. 304–5. Tesch, 1918, pp. 177–8. Balss, 1922, p. 113. Sakai, 1939, pp. 371, 372. Edmondson, 1954, p. 222 (in key).

Catoptrus Milne Edwards, A., 1870, p. 82. Ortmann, 1894, p. 685. Alcock, 1900, p. 307. Tesch, 1918, pp. 178–9. Sakai, 1939, p. 371. Edmondson, 1954, p. 222.

Goniocaphyra de Man, 1887*b*, p. 339.

As Tesch (1918, p. 178, under *Libystes*) has shown, there are no reasons to justify the continued maintenance of the genus *Catoptrus*. The characters which have been used for diagnostic purposes are the entirety or toothed nature of the anterolateral borders; the production or otherwise of the antero-external angle of the third maxillipeds; and the relative flattening of the fifth leg. Only the last seems to have any quality of generic exclusiveness. There are great differences in this feature within the species of the genus *Libystes* and since *Catoptrus* only slightly exceeds the range of form within *Libystes* it seems necessary to suppress the genus *Catoptrus*. Since *Libystes* and *Catoptrus* have each contained a species bearing the name *nitidus* some alteration of trivial names is necessary and *Catoptrus nitidus* A. Milne Edwards, 1870, becomes *Libystes truncatifrons* (de Man, 1887*b*).

Generic Description

Carapace.—Deepish, subquadrilateral or subelliptical, vastly broader than long, with little or no distinction of regions. Convex fore and aft, slightly so from side to side.

Fronto-orbital borders much narrower than the greatest breadth of the carapace, so that the anterolateral borders, which may be toothed or entire, have a cancroid-like curve. Front square-cut and quite straight, not well separated from the supra-orbital angles, slightly notched in the middle line, a third or less the greatest breadth of the carapace.

Orbits.—Shallow, their upper border entire.

Basal antennal joint.—Short, the antennal flagellum standing loosely in the orbital hiatus.

Antennules.—Folding transversely.

Buccal cavern.—Square-cut, much broader than long; the efferent branchial canals of the palate very well defined.

Third maxilliped.—Merus short and broad. In some species the external angle much produced, as in many species of *Portunus*.

Chelipeds.—Subequal, longer, and much more massive than the legs. Hands somewhat tumid and unequal in the adult.

Walking legs.—Slender, unarmed.

Fifth leg.—Forming a typical swimming paddle in some of the species, but not paddle-like in others.

Male abdomen.—Covering the whole width of the sternum between the last pair of legs. Third to fifth abdominal terga fused.

Key to the Indo-West-Pacific Species of Genus Libystes

1. Anterolateral border bearing teeth 2
Anterolateral border entire, without teeth 5

2(1). Fifth legs markedly flattened and paddle-like 3
Fifth legs not paddle-like 4

3(2). 6 or 7 anterolateral teeth (including the extra-orbital angle); front straight .... *L. edwardsi* Alcock (1900, p. 306), Alcock and McArdle (1902, pl. lxi, fig. 1) (not recorded from Australia)
5 anterolateral teeth (including the rounded extra-orbital angle); front curved .... *L. paucidentatus*, sp. nov.

4(2). Carapace relatively narrow (length : breadth ratio *c.* 1 : 1·4, excluding the last anterolateral teeth); first anterolateral tooth much broader than fifth; merus of third maxilliped longer than broad and slightly produced at antero-external angle .... ..*truncatifrons* (de Man) (1887*b*, p. 339, pl. 14, fig. 1) (not recorded from Australia)
Carapace relatively broad (length : breadth ratio *c.* 1 : 1·7, excluding the last anterolateral teeth); first and fifth anterolateral teeth subequal; merus of third maxilliped broader than long with antero-external angle greatly produced .... *L. inequalis* (Rathbun) (1906, p. 870, text fig. 29, pl. 12, fig. 9) (not recorded from Australia)

5(1). Borders of carapace and legs densely haired .... *L. villosus* Rathbun (1924, p. 127) (not recorded from Australia)
Borders of carapace and legs hairless 6

6(5). Carapace elliptical .... *nitidus* A. Milne Edwards (1868, p. 83, pl. 20, figs. 5-7) (not recorded from Australia)
Carapace subquadrilateral .... *L. alphonsi* Alcock (1900, p. 306), Alcock and McArdle (1902, pl. lxi, fig. 2) (not recorded from Australia)*

LIBYSTES PAUCIDENTATUS, sp. nov.

Fig. 1*B*, 2*D*; Plate 1, Fig. 4; Plate 5*D*

Material Examined

♂ 18 mm, Redland Bay, in gritty mud M.L.W., 11.viii.58, W.S. and B.C. (paratype). ♂ 14·5 mm (holotype), ♀ 15 mm (paratype), and ♀ 16 mm (allotype), Redland Bay, in gritty mud M.L.W., 7.i.59, B.C. The holotype and allotype are to be deposited in the Australian Museum and the paratypes in the Queensland Museum.

Material illustrated.—Holotype.

Description

Front.—Narrow (*c.* $\frac{1}{4}$ carapace width) and consisting of two slightly rounded lobes; inner orbital lobes indistinguishable.

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* Tesch (1918) and Edmondson (1954) both consider that *L. alphonsi* is probably a synonym of *L. nitidus*.

Anterolateral teeth.—Five, all blunt, of which the first is a flat protuberance, the fourth normally the smallest, and the fifth a projecting procurved spine.

Carapace.—Almost twice as broad as long (from 1·8 to 1·9 times), microscopically punctate over most of its surface, granular near the anterolateral borders. With a blunt eminence near each posterior angle and a slight concavity of the lateral epibranchial region to give the carapace a quadrilateral appearance.

Chelipeds.—With the right larger than the left in the males but equal in the females. The chelipeds are more than three times the length of the carapace and without carinae or spines except on the fingers. The arm bears lines of granules, especially on the upper surface, tending to a squamiform appearance. Fingers slender and hooked at the tip, equal to the length of the palm except in the smaller chelipeds of the males where they are longer. The opposed surfaces of the fingers are lined with small denticles amongst which there are occasional teeth, some 4 or 5 short ones on the movable finger and typically 3 elongate sharp ones on the immovable finger. Walking legs long and slender, fifth leg paddle-like, with the greatest length of the carpus less than half the greatest length of the propodus.

Male pleopods.—Little curved, evenly tapering to a pointed, obliquely cut tip. On the outer side there is a patch of bipinnate hairs just beyond the basal lobes, which thin out and almost fuse with a second band of long hair-like bristles commencing about half-way up the appendage. These bristles become shorter, stouter, and backwardly directed, and continue to the tip as a single row which tends to pass to the under surface, there fusing with the terminal armature. On the inner side just beyond the basal lobes there is a conspicuous tuft of long bipinnate hairs. Leading forward from this there are isolated hairs, which become more frequent and stouter, forming a row which ends just behind the tip. Apart from the row of recurved bristles on the outer side, the terminal armature consists only of short scattered spines on the under surface. A sparse row is distinguishable near the inner side of the under surface, and this becomes more concentrated and passes around just behind the proximal border to end on the upper surface.

Colour.—Dull brown.

Discussion

This species is close to *L. edwardsi* Alcock, 1900 (see also Alcock and McArdle 1902, pl. lxi, fig. 1).

It differs in the following particulars: (1) fewer anterolateral teeth; (2) rounded instead of straight front; (3) broader carapace; (4) lines of granules tending to form squamiform markings on the upper surface of the arm of the cheliped; (5) relatively smaller carpus of the fifth leg; (6) presence of teeth on both movable and immovable fingers of both chelipeds as against only on the immovable finger of the smaller cheliped.

The marked gap in the distribution between *L. edwardsi* and the present specimens also supports the idea that they are different species, the former having been recorded only from the Persian Gulf and the Andamans.

Genus CARUPA Dana

Carupa Dana, 1851, p. 129; 1852*a*, p. 85; 1852*b*, p. 279. Alcock, 1899, pp. 25–6 (synon.). Leene, 1938, p. 9 (synon.); 1940, p. 164.

CARUPA TENUIPES Dana

Plate 2, Fig. 1

Carupa tenuipes Dana, 1851, p. 129; 1852*a*, p. 85; 1852*b*, pp. 279–80. Leene, 1940, pp. 165–8, figs. 1, 2 (male pleopod).

Carupa laeviscula Heller, 1862, p. 520; 1865, p. 27, pl. 3, fig. 2. Alcock, 1899, p. 26 (synon.). Leene, 1938, pp. 9–10. Sakai, 1939, p. 373, pl. xliv, fig. 3 (coloured). Edmondson, 1954, pp. 266–7, figs. 3*b*, 4*e*, 4*f*, 4*g*.

Material Examined and Illustrated

♀ 26 mm, Hope I., Aug. 1913, A. R. McCulloch (Aust. Mus. Reg. No. P3800).

Description

General.—See key, plate, and description by Leene (1940).

Male pleopod.—Not available.

Distribution

From Madagascar (fide Leene 1940) to Hawaii (Edmondson 1954), but apparently not previously recorded from Australia.

Subfamily **MACROPIPINAE**, nom. nov.

KEY TO INDO-WEST-PACIFIC GENERA OF SUBFAMILY MACROPIPINAE

1. Front bearing spines .... *Ovalipes* Rathbun (1898)
Front bearing lobules or teeth 2
2(1). Dactyl of fifth leg lanceolate; carapace with transverse ridges .... *Macropipus* Prestandrea (1833)
Dactyl of fifth leg broadly oval; carapace without transverse ridges 3
3(2). Carapace smooth; arm short and without spines, legs stout ....*Benthochascon* Alcock & Anderson (1899, p. 10) (not recorded from Australia)
Carapace with definitely disposed tubercles; arm longish and with a spine or spines; legs slender .... *Parathranites* Miers (1886, p. 186 under *Lupocyclus* (*Parathranites*) *orientalis*) (not recorded from Australia)

Genus OVALIPES Rathbun

Platyonichus Latreille, 1825, p. 151.

non *Platyonichus* Latreille, 1818, p. 4 (emend. pro *Portumnus* Leach, 1814).

Anisopus de Haan, 1833, pp. 3, 12.

non *Anisopus* Meigen, 1803, p. 264. (Diptera.)

Platyonychus Voigt, 1836, p. 104. Dana, 1851, p. 130. Miers, 1886, pp. 201–2.

Ovalipes Rathbun, 1898, p. 597; 1930, pp. 18–19. Sakai, 1939, p. 374. Barnard, 1950, p. 150.

Aeneacancer Ward, 1933, p. 381. McNeill, 1953, p. 93.

Platyonichus and its misspelling *Platyonychus* are in the Official Index of Rejected and Invalid Generic Names in Zoology (Internat. Comm. Zool. Nom. 1958, Direction 84, pp. 109–10, names 1091, 1092). *Anisopus* de Haan is preoccupied and *Ovalipes* is thus the first acceptable name.

The genus *Aeneacancer* was created by Ward for his species *A. molleri*. After comparison with *O. ocellatus* (Herbst, 1799) from America, Ward detailed six features distinguishing his genus. As McNeill (1953) has pointed out *A. molleri* is much closer to *O. iridescens* (Miers 1886) than to *O. ocellatus*. Ward's six features, with comments thereon, are as follows:

(1) Presence of two transparent areas near the posterior margin of the dorsal surface of the carapace. There are suggestions of similarity in Miers's (1886, pl. xvii, fig. 2) and Sakai's (1939, pl. xlii, fig. 4) plates of *O. iridescens*.

(2) Presence of a stridulatory mechanism. According to Rathbun (1930, p. 19) a similar mechanism is present in the species of *Ovalipes* Ward used for comparison—*O. ocellatus*.

(3) More robust third maxillipeds, with merus only slightly produced at the antero-external angle. This is comparable with Miers's original description of *O. iridescens* (see Miers 1886, p. 203).

(4) Larger orbits. This does not apply if *O. iridescens* is used for comparison.

(5) Regions of the carapace more deeply marked. This feature is possibly valid.

(6) Fronto-orbital region equal to half the carapace width, and produced beyond the outline of the anterolateral margin. This again does not apply if *O. iridescens* is used for comparison.

One is left with a single relative feature, viz. more deeply marked regions of the carapace, as justification for the separateness of the genus. Against this, additional features are shared between *A. molleri* and *O. iridescens*. McNeill (1953) has commented on the iridescent sheen of the carapace, and in addition the armature of the immovable fingers of the chelipeds is similar in the two species. Either *Aeneacancer* should disappear into the synonymy or *O. iridescens* should be transferred to Ward's genus. Having no specimens of *O. iridescens* for comparison, the present authors prefer to take the former alternative.

KEY TO INDO-WEST-PACIFIC SPECIES OF GENUS OVALIPES

1. Anterolateral teeth broad and narrowly separated; a strong tooth on upper margin of orbit . . . . *O. punctatus* (de Haan) (1833)
Anterolateral teeth consisting of narrow, well-separated spines, no tooth on upper margin of orbit 2

2(1). Front bearing 3 spines; no transparent areas in mesobranchial portion of carapace . . . . . . *O. iridescens* (Miers) (1886, p. 202, pl. xvii, fig. 2) (not recorded from Australia)
Front bearing 4 spines; conspicuous transparent areas in mesobranchial portion of carapace . . . . *O. molleri* (Ward) (1933)

OVALIPES PUNCTATUS (de Haan)

Figs. 1*C*, 2*E*; Plate 2, Fig. 2; Plate 5*E*

Corystes (*Anisopus*) *punctatus* de Haan, 1833, p. 44, pl. 2, fig. i.
Platyonichus bipustulatus Milne Edwards, H., 1834, p. 437, pl. 17, figs. 7–10.
Platyonichus bipustulatus Milne Edwards, H. Haswell 1882*b*, pp. 84–5.
Ovalipes bipustulatus (Milne Edwards, H.). Rathbun, 1898, p. 597. Hale, 1927, pp. 147–8, fig. 148. Ward, 1929, p. 79 (record only).
Ovalipes punctatus (de Haan). Rathbun, 1930, pp. 24–7, pls. 5–8 (synon.). Sakai, 1939, pp. 374–5, pl. xlii, fig. 3 (coloured). Barnard, 1950, pp. 150–2, figs. 27*a*, 29*a–d*.

Material Examined

42 ♂♂ (12–97 mm); 23 ♀♀ (27–85 mm); 2 sex indetermined (30, 90 mm). Additional specimens were more cursorily examined.

QUEENSLAND: Wide Bay, Point Lookout (Stradbroke I.), Miami Beach. NEW SOUTH WALES: Yamba, Port Stephens, Newcastle, Cudgee Beach, Broken Bay, Pitt Water, Manly, Port Jackson, Sydney Heads, Maroubra Bay, Botany Bay, Gunnamatta Bay, Lake Illawarra, Shoalhaven R., Jervis Bay. LORD HOWE ISLAND. VICTORIA: Port Phillip Heads, Frankston, Mentone, Beaumaris, Brighton, Queenscliffe, Lonsdale. TASMANIA: King I., Cole's Bay, Dunally, Seven Mile Beach (Frederick Henry Bay), Cowrie Point, Stewart Bay. SOUTH AUSTRALIA: Gulf St. Vincent, Sellicks Beach, Vivonne Bay. WESTERN AUSTRALIA: King George Sound, Carnac I., Leighton, Cottesloe.

Recorded habitats.—Surf beaches (attacking angler's bait), swimming and burrowing in surf sand at L.W.M., dredged 16–19 fm, trawled 8 fm, washed up on beach, on reef (Lord Howe I.), sand flats in shallow water.

Material illustrated.—Carapace: ♀ 51 mm, Miami Beach, S. Qld., 22.viii.53, B. Winks (At Zool. Dept. Univ. Qld.). Male abdomen: ♂ 70 mm, Stewart Bay, Tasman Peninsula, 13.iv.52 (at Tasmanian Museum, Hobart). Male pleopod: ♂ 39 mm, Seven Mile Beach, Tas., V. V. Hickman, Jan. 1956 (at Zool. Dept. Univ. Qld.).

Description

General.—Considered unnecessary.

Male pleopod.—Only slightly curved and tapering gently. Beyond the basal lobes a row of bipinnate hairs on both outer and inner sides extends up the appendage to end a quarter of the way back from the tip. A separate upper row is present on the inner side in the proximal quarter. Terminal armature on the outer side consists of a narrow band of backwardly directed spinules which commences before the bipinnate hairs end, becomes denser, and spreads to the under surface, terminating just behind the tip.

On the inner side a scattered band on the under surface originates about half-way along the appendage and extends to the upper surface, ending just short of the tip.

Distribution

Indo-West-Pacific from South Africa to Japan and New Zealand; East Pacific from Juan Fernandez, Peru, and Chile; South Atlantic from Argentine and Uruguay (Rathbun 1930).

Common throughout the southern half of Australia with present records extending the range to Queensland and West Australia. Past Australian records are given by Haswell (1882*b*), Miers (1886), Stead (1898), Whitelegge (1900), Hale (1927), Ward (1929), Rathbun (1930), and Anderson (1938).

OVALIPES MOLLERI (Ward), comb. nov.

Figs. 1*D*, 2*F*; Plate 2, Fig. 3; Plate 5*F*

Aeneacancer molleri Ward, 1933, pp. 381–3, pl. xxiii, fig. 11. McNeill, 1953, p. 93, pl. 7, figs. 1, 2.

Material Examined

28 ♂♂ (53–93 mm); ♀ 67 mm.

NEW SOUTH WALES: S. of Montague I., off Broken Bay. VICTORIA: 20 miles W. of Babel I., Bass Strait.

Recorded habitats.—20–120 fm.

Material illustrated.—♂ 93 mm, off Broken Bay, N.S.W., 120 fm, Capt. K. Moller (Aust. Mus. Reg. No. P10730, part).

Description

General.—See discussion following generic synonymy and also key. The following combination of characters is diagnostic: (1) The iridescence; (2) the semi-transparent areas on the carapace; (3) the spines (four or five) on the immovable finger of the chela; (4) the four frontal spines; and (5) the stridulating ridge of elongated granules "parallel to and just below the line of demarcation between the subhepatic and pterygostomial regions" (Ward 1933, p. 382).

Male pleopod.—Extremely stout, evenly curved with a short base, a gradually tapering neck, and a slightly flared tip. Beyond the basal lobes on the outer side is a dense row of very long bipinnate hairs extending for seven-eighths the length of the appendage. On the inner side a similar row of shorter hairs terminates about a quarter of the way back from the tip. The terminal armature on the outer side consists of a band of small backwardly directed spinules commencing just before the termination of the bipinnate hairs, and continuing almost to the tip. On the inner side a thinner band extends from the end of the bipinnate hairs, terminating a short distance back from the tip. On the under surface of the base on the inner side there is a wide sparse band of small spinules, which widens out about half-way up the appendage to give a sparse covering to the whole under surface. It then narrows again a short distance past the end of the series of bipinnate hairs on the outer side. This band merges with the terminal armature on the outer side.

Distribution

Only from moderately deep water off the south-east of Australia. The next closest species *O. iridescens* has been infrequently recorded by Miers (1886), Yokoya (1933), Leene (1938), and Sakai (1939), in an area extending from Japan to the west of New Guinea. Again moderately deep water is mentioned.

Genus MACROPIPUS Prestandrea

Macropipus Prestandrea, 1833, p. 5. Internat. Comm. Zool. Nom., 1956, pp. 317–36.
Portunus Milne Edwards, A., 1861, p. 392. Balss, 1922, p. 101. Sakai, 1939, p. 377.
"*Portunus*" Palmer, 1927, pp. 879–81.
non *Portunus* Weber, 1795, p. 93. Fabricius, 1798, pp. 325, 363. Rathbun, 1897, p. 155. Hale, 1927, p. 149. Rathbun, 1930, p. 33. Edmondson, 1954, p. 235. Stephenson and Campbell, 1959, p. 85.
Liocarcinus Stimpson & Pourtalès, 1870, p. 146. Rathbun, 1897, p. 155; 1902, p. 25. Stimpson, 1907, p. 74. Parisi, 1916, p. 170. Urita, 1926, p. 3. Hale, 1927, p. 148. McNeill and Ward, 1930, p. 379. Guiler, 1952, p. 39.

The use of the present unfamiliar generic name, to replace the familiar "*Portunus*" of European workers and *Liocarcinus* of Australian workers is due to a decision of the International Commission on Zoological Nomenclature (1956).

Only one species occurs in the Indo-West-Pacific.

MACROPIPUS CORRUGATUS (Pennant)

Figs. 1*E*, 2*G*; Plate 2, Fig. 4; Plate 5*G*

Cancer corrugatus Pennant, 1777, p. 5, pl. v, fig. 9.

Portunus corrugatus (Pennant). De Haan, 1833, p. 40. Miers, 1879, p. 34; 1886, p. 200. Ortmann, 1893, p. 70. Fulton and Grant, 1906, p. 18.

Portunus strigilis Stimpson, 1858, p. 38 (fide Sakai 1939).

Portunus subcorrugatus Milne Edwards, A., 1861, p. 402, pl. xxxvi, fig. 2. Nobili, 1906, pp. 186–7.

Liocarcinus strigilis (Stimpson). Rathbun, 1902, p. 25. Stimpson, 1907, p. 74, pl. ix, fig. 6. Parisi, 1916, p. 170. Urita, 1926, p. 3.

Portunus corrugatus strigilis Stimpson. Balss, 1922, p. 101. Yokoya, 1933, p. 173. Sakai, 1934, p. 301; 1936, p. 128, pl. 32, fig. 1 (coloured); 1939, p. 377, pl. xliii, fig. 1 (coloured).

Liocarcinus corrugatus (Pennant). Hale, 1927, p. 148, fig. 149. McNeill and Ward, 1930, pp. 379–80. Guiler, 1952, p. 39.

"*Portunus*" *corrugatus* (Pennant). Palmer, 1927, pp. 881–2, fig. 2*A–H*, pp. 899–900 (discussion *P. subcorrugatus* and *P. strigilis*).

(?)*Portunus corrugatus* (Pennant). Borradaile, 1916, p. 98, fig. 9 = *P. borradailei* Bennett, 1930, pp. 256–7, figs. 1–4.

The complex synonymy arises from two causes, first from alterations in generic names and secondly from real doubts concerning the degree of separation of the different closely allied forms from various parts of the world. Five such have been considered in the past.

(1) The European forms, probably more exactly the Plymouth ones, described by Palmer (1927). These are undoubtedly the same as Pennant's originals. Here there is tolerably continuous distribution from Scotland to Cape Verde, the Azores, the Canary Islands, the Mediterranean, and the Adriatic. Apparently no studies have been made of possible structural variations within this extensive range, along the lines of the comparison of Channel and Mediterranean populations of *Carcinus* by Demeusey and Veillet (1953).

(2) The Japanese forms, described as *P. strigilis* by Stimpson. The Japanese workers, leading up to Sakai (1939), have recognized the distinctness of their forms, by virtue of their possessing a relatively narrower carapace and more strongly marked regional boundaries (Borradaile 1916, p. 97 and Rathbun in Palmer 1927, footnote p. 900). The most recent tendency has been to give this form subspecific status.

(3) The Red Sea forms, described as *P. subcorrugatus* by A. Milne Edwards (1861). Rathbun (in Palmer 1927) considers they fall within the variability of the typical *P. corrugatus*.

(4) The Australian forms. These were mentioned by Borradaile (1916, p. 97) and have been dealt with by Hale (1927) and by McNeill and Ward (1930). Although the carapace regions are more strongly marked, and probably the carapace is relatively narrower than in the British specimens, none of the above workers separated

them either specifically or subspecifically from Pennant's species. It would require a much greater range of Australian material than the present authors have had access to, and also a detailed study of the Northern Hemisphere populations, before the question of separateness finally could be decided. The present authors have considered it advisable to "lump" European, Japanese, Red Sea, and Australian specimens.

(5) The New Zealand forms. Bennett (1930) thinks that these deserve specific status by virtue of the straight-sided male abdomen. In the distinctness of the carapace regions and the relative narrowness of the carapace they appear to resemble the Australian forms. It is unfortunate that this species is based upon a single badly preserved juvenile, especially so when the basis for comparison is with specimens "which approached the maximum size found in the species" (Palmer 1927, p. 878).

Material Examined

6 ♂♂ (6–21 mm); 6 ♀♀ (6–26 mm).

NEW SOUTH WALES: Jervis Bay, Botany Bay, Green Cape, Gunnamatta Bay. VICTORIA: Port Phillip, Cape Everard. TASMANIA: Wineglass Bay.

Recorded habitats.—Trawled, 40–75 fm; hand-netted in weed on tidal flat.

Material illustrated.—♂ 21 mm, Gunnamatta Bay, pres. March 1947, Miss E. Pope (Aust. Mus. Reg. No. P11729).

Description

General.—The species is clearly recognizable from the keys, figures, and Palmer's description (Palmer 1927, pp. 881–2, figs. 2*A–H*). In the Australian specimens the carapace regions are strongly marked and the carapace is relatively narrow.

Male pleopod.—Regularly tapering to an unflared tip bent practically at right angles to form a sickle shape. Proximal two-thirds on the outer border bears very long bipinnate hairs, and on the inner side a proximal area of shorter hairs on the upper surface which extends around the inner border to the under surface. Microscopic spinules on the upper surface begin a quarter of the way back from the tip and extend to both borders, more being visible in profile view on the inner border than on the outer. On the under surface microscopic spinules begin about a quarter of the way back and increase in size and density to form a fairly dense patch of backwardly directed spinules ending just behind the tip.

Palmer's (1927) figure (2*E*) is inadequate for purposes of comparison.

Comments

Palmer (1927, p. 904) states that *P. corrugatus* approaches the primitive form of the genus, with little modification of the merus of the fifth legs for swimming. He notes affinities with *Nectocarcinus integrifrons* and the genus *Bathynectes*, and suggests that almost world-wide distribution is indicative of primitiveness in this species as in *Carcinus maenas*.

Distribution

Published and present records within Australia are from Tasmania (Miers 1886, repeated Guiler 1952), Victoria (Miers 1886; Fulton and Grant 1906), South Australia (Hale 1927), New South Wales (McNeill and Ward 1930).

Palmer (1927) gives its distribution as "British Isles, France, Belgium, Mediterranean, Adriatic, Canary Is. (Heller 1863); Scotland to Cape Verde, Azores, and Canaries (Bouvier 1922); Oran (Lucas 1849); Red Sea (A. Milne Edwards 1861); Senegambia (Miers 1881); Senegambia to Sierra Leone (Balss 1922); Japan (Miers 1879); Victoria, Australia (Miers 1886); New Zealand (Borradaile 1916)". The doubtful status of the last record has been discussed.

Subfamily **CAPHYRINAE** Alcock, 1899

KEY TO INDO-WEST-PACIFIC GENERA OF SUBFAMILY CAPHYRINAE

1. Front produced into a blunt projecting lobe; propodus of fifth leg subcircular ....*Coelocarcinus* Edmondson (1930, p. 13) (not recorded from Australia)
Front not produced into a projecting lobe; propodus of fifth leg not subcircular ..2

2(1). Fifth legs turned back dorsally over carapace 3
Fifth legs not turned back dorsally over carapace 4

3(2). Front, upper border of orbit, and anterolateral borders lamellate; carpus of fifth legs much broader than propodus. (Wrist and hand of chelipeds markedly carinate, carapace very convex) ....*Sphaerocarcinus* Zehntner (1894, pp. 163–4) (not recorded from Australia)
Front, upper border or orbit, and anterolateral borders not lamellate; carpus of fifth legs not broader than propodus ....*Caphyra* Guérin (1832) (most spp.)

4(2). Dactylus of fifth pair of legs paddle-shaped ....*Lissocarcinus* Adams & White (1849)
Dactylus of fifth pair of legs claw-shaped ....*Caphyra* Guérin (1832) (some spp., but none recorded in Australia)

Genus LISSOCARCINUS Adams & White

Lissocarcinus Adams & White, 1849, p. 45. Alcock, 1899, p. 18. Leene, 1938, pp. 3–5 (synon.). Sakai, 1939, p. 378. Barnard, 1950, p. 145.

The genus is adequately described by Leene (1938) who gives keys to the eight Indo-West-Pacific species.

KEY TO AUSTRALIAN SPECIES OF GENUS LISSOCARCINUS

(adapted from Sakai (1939))

Dorsal surface of carapace rather flat; front medially notched; supra-orbital angles well defined; anterolateral teeth acuminate; without bold colour patterning ....*L. polybioides* Adams & White (1849)
Dorsal surface convex in central area; front entire; supra-orbital angles obscurely defined; anterolateral teeth blunt and confluent; with bold light and dark colour patterning ....*L. orbicularis* Dana (1852*a*)

LISSOCARCINUS POLYBIOIDES Adams & White

Figs. 1*F*, 2*H*; Plate 3, Fig. 1; Plate 5*H*

Lissocarcinus polybioides Adams & White, 1849, p. 46, pl. 11, fig. 5. Haswell, 1882*b*, p. 83. Miers, 1886, p. 205. Alcock, 1899, pp. 19–20 (synon.). Rathbun, 1911, p. 284. Hale, 1927, p. 146. McNeill and Ward, 1930, pp. 378–9, pl. lix, fig. 4. Leene, 1938, pp. 6–7. Monod, 1938, p. 113, fig. 9. Sakai, 1939, p. 379, pl. xliii, fig. 3 (coloured).

Material Examined

5 ♂♂ (6–19 mm), 4 ♀♀ (13–20 mm). Smallest ovigerous ♀ 14 mm. Ovigerous ♀♀ from months of February and October.

QUEENSLAND: Holbourne I., Bowen Harbour, Middle I. (Port Denison), Port Molle. NEW SOUTH WALES: Port Jackson, Newcastle. WESTERN AUSTRALIA: Roebuck Bay.

Recorded habitats.—In branches of live coral; dredged 5–9 fm; trawled.

Material illustrated.—Dorsal view. ♀ (ovigerous) 14 mm, off Middle I., Port Denison, pres. February 1924, E. H. Rainford (in branches of live coral) (Aust. Mus. Reg. No. P6999). Male pleopod: ♂ 16 mm, Holbourne I., Port Denison, pres. July 1918, E. H. Rainford (Aust. Mus. Reg. No. P4189).

Description

General.—Considered unnecessary.

Male pleopod.—Base robust; shaft straight and untapered, curving outwards at the extreme tip. A membrane is attached to the outer edge of the distal half of the shaft and projects over the inner edge. Beyond the basal lobes bare except for an occasional hair until near the tip. Subterminally on the under surface there are minute scattered spinules.

The terminal armature, which is reminiscent of a cockatoo's crest, consists of a row of very long, straight, evenly tapered bipinnate bristles on the inner margin, extending from the upper edge of the membrane right around the tip.

The present structure shows resemblances to Edmondson's (1954) figures 7*b* and 7*e* of *Lissocarcinus laevis* Miers (1886). In these figures, however, the bristles towards the tip of the appendage are decreasing progressively in size.

Distribution

From the Seychelles (Rathbun 1911) to Japan (Sakai 1939) and Australia. Previous Australian records are from Port Denison, Port Molle (McNeill and Ward 1930), Port Jackson (Haswell 1882*b*); and South Australia (Miers 1884; Hale 1927).

LISSOCARCINUS ORBICULARIS Dana

Plate 3, Fig. 2

Lissocarcinus orbicularis Dana, 1852*a*, p. 86; 1852*b*, p. 288, pl. xviii, figs. *a–e*. Alcock, 1899, pp. 20–1 (synon.). Leene, 1938, p. 7. Sakai, 1939, pp. 379–80, pl. xlv, fig. 1 (coloured). Barnard, 1950, pp. 145–6, fig. 28*g*. Edmondson, 1954, p. 230, fig. 6*b*.

Material Examined and Illustrated

♀ 8 mm, from surface *Holothuria atra*, Jaeger, outer banks at Dunwich, Moreton Bay, Queensland, coll. D. McColm, 5.x.58.

Description

General.—Considered unnecessary.

Distribution

The only previous Australian record is from Murray I., Queensland (Calman 1900). The species is known from South Africa (Barnard 1950) and the Red Sea (Monod 1938) to Hawaii (Edmondson 1954).

Genus CAPHYRA Guérin

Caphyra Guérin, 1832, pp. 285, 286–7. Milne Edwards, A., 1873, p. 172. Haswell, 1882*b*, p. 82. Nobili, 1901, p. 11; 1906, p. 188. Balss, 1934, p. 506. Leene, 1938, pp. 8–9.

Some 16 species of this typically commensal genus have been described from the Indo-West-Pacific. Prior to the present work only three were known from Australian waters, and one of these must disappear into the synonymy. Two additional species (one new) are recorded below.

The genus is a difficult one because many of the features generally used to distinguish species of portunids here vary within a given species. This applies particularly to the nature of the front and the anterolateral borders. A complete revision of the genus is desirable, and in this emphasis would no doubt be placed upon the first male pleopods and the shape of the propodus and dactylus of the last walking legs. Gordon (1941) was the first to employ these features, which show marked differences from species to species.

The experience of the authors suggests that coloration of the live specimens is diagnostic, and also that the species have marked host preferences. These essential details are rarely given in the older descriptions, and in revising the group, collection and examination of living topotypical material would be desirable.

In describing the fifth legs, difficulties arise over orientation. Because in most species these legs are directed forward above the carapace, what is normally the posterior surface becomes the anterior. There are further complications due to flexion of the legs, sometimes with the ultimate segment reversed in orientation compared with the rest of the leg. In the present work the terms "inner" and "outer" are employed, the former being the inside of the curve made by the appendage *in situ*, and being morphologically equivalent to "posterior" in other genera.

In measurements of the fifth legs, the breadths of segment are the maximum breadths, and lengths are from the distal extremity to the centre of the articulation in a straight line.

KEY TO THE INDO-WEST-PACIFIC SPECIES OF GENUS CAPHYRA

1. Fifth pair of legs not turned back dorsally over the carapace 2
Fifth pair of legs turned back dorsally over the carapace 3

2(1). Anterolateral margins toothed ....
....*C. natatrix* Zehntner (1894, p. 162, pl. vii, fig. 10) (not recorded from Australia)
Anterolateral margins entire ....
..................*C. archeri* Walker (1887, p. 116) (not recorded from Australia)*

3(1). Front composed of rounded lobes or sinuous (effectively bilobed) 4
Front composed of teeth 9

4(3). Carapace circular in outline and markedly convex ....
C. hemisphaerica Rathbun (1911, p. 204, pl. 15, fig. 9) (not recorded from Australia)
Carapace not as above 5

---

* Balss (1934, p. 506) suggests this species should belong to the oxyrhynchids, not the portunids.

5(4). 2 anterolateral teeth (the second very conspicuous) .... *C. unidentata* Lenz (1910, pp. 555–6, figs. 2, 3, 4) (not recorded from Australia)

More than 2 anterolateral teeth (usually four) 6

6(5). Front extended and smoothly rounded except for a small median notch .... *C. rotundifrons* (A. Milne Edwards) (1869)

Front not as above 7

7(6). Propodus of fourth walking leg elongate, length more than thrice breadth 8

Propodus of fourth walking leg broad, length less than thrice breadth .... *C. alcyoniophila* Monod (1928, pp. 4–10, figs. 1–4) (not recorded from Australia)

8(7). Hand of cheliped with 2 parallel carinae .... *C. yookadai* Sakai (1933)

Hand of cheliped with 1 dorsal carina, interrupted by a spine ...... *C. fulva*, sp. nov.

9(3). Front, excluding inner orbital lobes, four-toothed 10

Front, excluding inner orbital lobes, six-toothed 11

10(9). Hand costate but spineless; 4 anterolateral teeth .... *C. alata* Richters (1880, p. 154, pl. xvi) (not recorded from Australia)

Hand with costae and spines; 3 anterolateral teeth .... *C. rouxi* Guérin (1832, pp. 287–9, pl. viii*A*) (not recorded from Australia)

11(9). Carapace smooth over most of its surface 12

Carapace closely granulated (4 anterolateral teeth) .... *C. monticelli* Nobili (1901, pp. 10–11) (not recorded from Australia)

12(11). 5 or 6 anterolateral teeth 13

4 anterolateral teeth 14

13(12). Front relatively straight .... *C. laevis* (A. Milne Edwards) (1869)

Front advanced *C. suvaensis* Edmondson (1935, p. 24, fig. 6) (not recorded from Australia)

14(12). Three ridges on carapace .... *tricostata* Richters (1880, p. 154, pl. xvi) (not recorded from Australia)

Single ridge on carapace 15

15(14). A spine on the external face of the hand near the wrist articulation 16

No spine on the external face of the hand near the wrist articulation .... *C. polita* (Heller) (1861, p. 359, pls. iii, iv) (not recorded from Australia)

16(15). Host *Xenia* .... *C. laevis* (A. Milne Edwards) (1869) (unusual specimen, see p. 98)

Host *Pinna* .... *C. octodentata* Balss (1934, p. 506) non Haswell (1882*a*) (not recorded from Australia)

Caphyra laevis (A. Milne Edwards)

Figs. 1*G*, 2*I*, 3*D–G*, 3*J*; Plate 3, Fig. 3; Plate 5*I*

Goniosoma laève Milne Edwards, A., 1869, p. 152.

Caphyra laevis (Milne Edwards). Milne Edwards, A., 1873, pp. 173–4, pl. iv, figs. 2*a–c*. De Man, 1887*b*, pp. 377–8. Nobili, 1901, p. 12 (key only, corrected 1906, p. 188). Grant and McCulloch, 1906, p. 18. McNeill, 1926, p. 307. Balss, 1938, p. 30. Leene, 1938, p. 9. Gordon, 1941, pp. 126–7, figs. 1, 2, 3*b*.

Caphyra octodentata Haswell, 1882*a*, pp. 753–4; 1882*b*, pp. 82–3. Nobili, 1901, p. 12 (key only, corrected 1906, p. 188).

Caphyra semigranosa de Man, 1887*b*, pp. 337–8. Nobili, 1901, p. 12 (corrected 1906, p. 188). (See Leene, 1938, p. 9. Gordon, 1941, pp. 126–7.)

Material Examined

21 ♂♂ (5–17 mm); 25 ♀♀ (6–21 mm). Smallest ovigerous ♀ 13 mm; ovigerous ♀♀ from Jan., Apr., Sept., and Dec.

QUEENSLAND: Murray I., Howick I., Whitsunday I., Dunk I., Capricorn Group (Masthead I., North West I., Heron I.), Dunwich.

Recorded habitats.—In *Xenia* on reef flats or from low water mark.

Material illustrated.—Whole carapace: ♀ 16 mm, N. side Heron I., middle of reef flat, 15.viii.50, W.S. (at Zool. Dept. Univ. Qld.). Male abdomen and fifth legs: ♂ 13 mm, Dunwich, commensal among *Xenia*, 18.viii.55 (at Zool. Dept. Univ. Qld.). Male pleopods: ♂ 11 mm, North West I., F. A. McNeill, April 1933 (Aust. Mus. Reg. No. P10376). Front: Fig. 3*D*, ♀ 12 mm, Heron I., in *Xenia*, 7.i.59, W.S. Fig. 3*E*, ♀ 12 mm, other data as last specimen. Fig. 3*F*, ♀ 14 mm, other data as last specimen. Anterolateral teeth: ♂ 5 mm, other data as last specimen.

Description

Front.—With 6 teeth normally clearly demarkated, rounded, and protruding (see Fig. 3*D*), but occasionally the 3 teeth on each side tend to fuse, thus giving 2 sinuous lobes, one on either side (see Fig. 3*E*). Alternatively the median and submedian teeth on each side coalesce, giving a quadrilobed front (see Fig. 3*F*).

Inner orbital lobes large, clearly separated from the frontal lobes.

Anterolateral teeth.—Typically 5; stout and sharply pointed; the first 3 larger than the last 2. In some specimens the fourth tooth is extremely small and in some the first 4 teeth are blunt (see Fig. 3*G*). (Gordon (1941) notes that one specimen from Masthead I. has the fourth anterolateral tooth absent on the left and vestigial on the right.)

Carapace.—Convex, broader than long, shiny. A pair of mesogastric ridges is clearly visible on some specimens but indistinguishable on others. In all cases, epibranchial ridges are well developed. The anterior half of the carapace is microscopically punctate, and this is clearest in the smallest specimens.

Chelipeds.—Right slightly larger than left and microscopically granular. Anterior border of arm with 3–5 blunt flattened spines; under surface of arm entire. Hand with only one carina on the inner margin of the upper surface, this carina being interrupted just beyond a single large spine which occurs not quite half-way along.

Legs.—Elongate and slender. The fifth, which is turned back over the dorsal surface, has the propodus roughly twice as long as broad (2·1 times), and has long fringing hairs on its inner and shorter ones on its outer surface. Dactyl slightly shorter than the propodus (0·8 times), reasonably broad (3·1 times as long as broad), flattened, lanceolate, and of a moderately typical portunid shape. Fringing hairs are present on both sides, those on the inner side being longer, and the distal eighth of the segment is bare.

Male pleopod.—Short, straight, and untapered, ending in a widely flared spoon-shaped tip set at an angle to the shaft of the appendage. Beyond the basal lobes, bare on the outer side. On the inner side *c.* 10–12 bristles are visible a short way up from the base, and a sparse series, which begins about half-way back from the tip, merges with a clump on the proximal edge of the flared tip. On the outer side just behind the tip 6–12 bristles are visible in profile view, these being part of a band on the distal half of the under surface of the flared area. On the upper surface the proximal end of the flared tip bears a row of bristles. A second upper series arises from the inner surface and curves to meet the previous row.

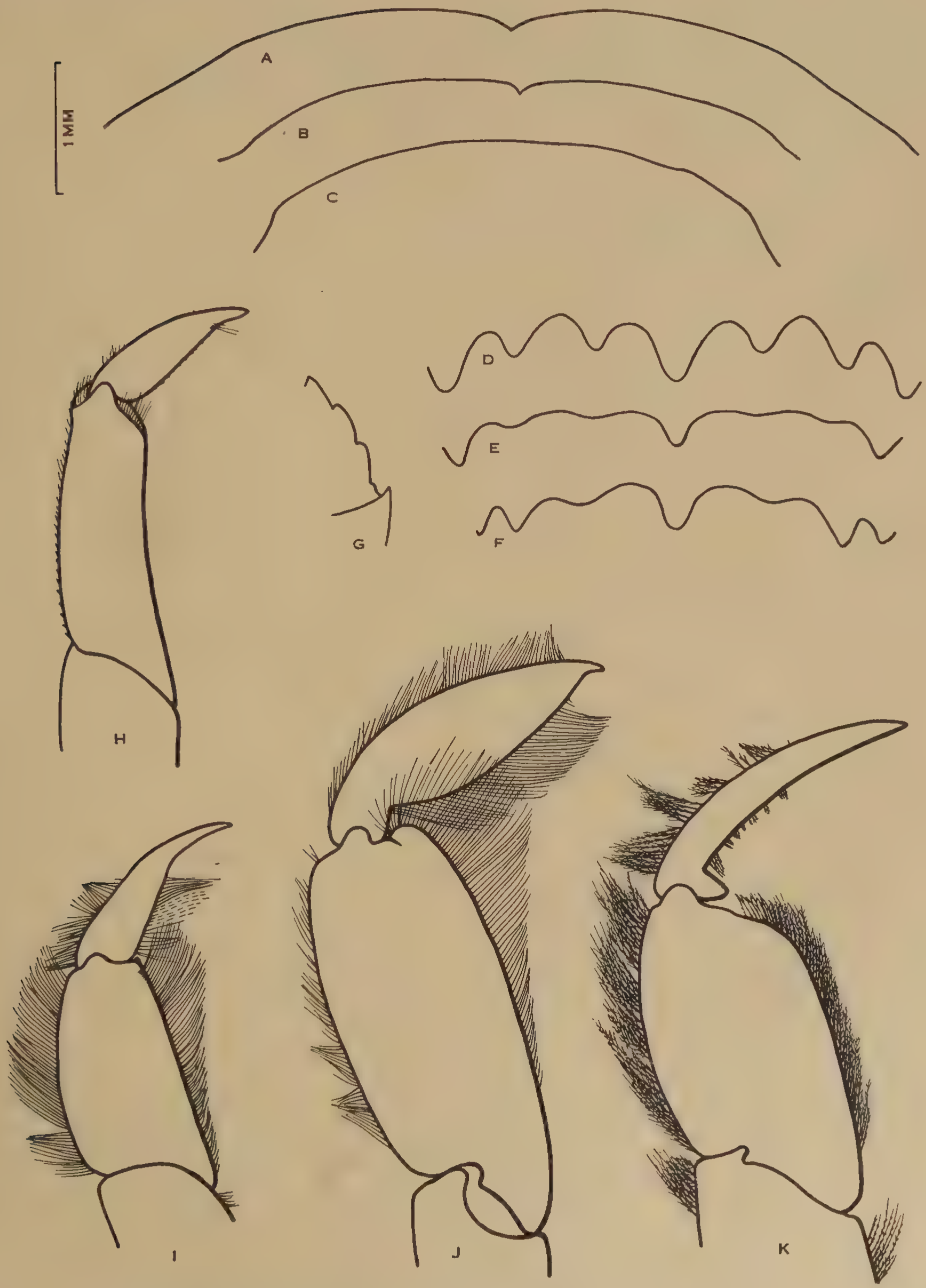

Fig. 3.—*A–G*.—Variation in the front of *Caphyra rotundifrons* (*A–C*), in the front of *C. laevis* (*D–F*), and in the anterolateral teeth of *C. laevis* (*G*). *H–K*.—Terminal segments of the right fifth legs of *H*, *C. yookadai*; *I*, *C. fulva*; *J*, *C. laevis*; *K*, *C. rotundifrons*. All drawings were made to the same scale.

Colour.—Background colour cream or light grey. Typically with six longitudinal marks in grey or greenish grey, each with a lighter central area. The lateral marks expand opposite the first three anterolateral teeth, the median marks are the shortest, and all are more conspicuous in the region anterior to the epibranchial ridge. Sometimes specimens are without markings, and have a uniform cream colour shortly after collection.

Comments

Of the 31 specimens examined while making the final description, eight contained branchial parasites causing distortion on the left of the animal, and four causing distortion on the right.

One of the Australian species of *Caphyra*, *C. octodentata* Haswell (1882*a*) remains obscure in spite of the present work. The type was placed in the Macleay Museum, University of Sydney, but is no longer there, nor is it in any other museum in Australia. There is no record of whether the species was based upon a single specimen or several, and no further specimens referable to this species have appeared in later collections from Australia. No record of the habitat was given. The species is distinguished from *C. laevis* solely by having four anterolateral teeth on each side instead of five.

There are three possibilities:

(1) Haswell made a simple error in misstating the number of teeth; possibly he excluded the first tooth or outer orbital lobe. Although this seems unlikely on the face of it, he almost certainly made a similar misstatement in describing his only other"new" species in this family (*Neptunus tomentosus* Haswell, 1882*a*, p. 547; see Stephenson and Campbell, 1959, p. 101).

(2) He was dealing with an unusual specimen of *C. laevis*. As already stated, Gordon (1941) obtained a specimen of *C. laevis* with only four anterolateral teeth on one side. However no truly and symmetrically four-toothed individual has appeared in Australian collections since Haswell's time.

(3) He examined an undescribed habitat which has been passed over by subsequent Australian workers. Balss (1934) has recorded *C. octodentata* from *Pinna* in Madagascar, and while the authors have not examined *Pinna* from the type locality of *C. octodentata* (Palm I., Queensland), numerous specimens from Moreton Bay have failed to reveal any *Caphyra*.

Of these three possibilities, the authors incline to the first, being influenced by the fact that Haswell did not list *C. laevis* in the Australian crustacean fauna. This is a common species, often obtained in student collections. It would be extraordinary for Haswell to find a new species which nobody else in Australia has since collected, and simultaneously pass over the most obvious species in the genus. It would be even more extraordinary for him to find a four-toothed *C. laevis* as his first and only specimen of that species. If *C. octodentata* Haswell is a synonym of *C. laevis*, problems arise regarding *C. octodentata* Balss. Although no extended description was given by Balss, he states that his specimen agrees with Haswell's description excepting that the spine at the articulation of the carpus and propodus occurs on the carpus instead of on the propodus as Haswell described. The spectacular feature of Balss' specimen was that it came from within *Pinna nigra*.

The habitat of *C. laevis* in Australia is restricted to amongst the polyps of the dove-grey soft coral, *Xenia*. If *C. octodentata* Haswell is the same as *C. laevis*, it would appear, from a consideration of habitat alone, that *C. octodentata* Balss is a different species. Obviously Balss's specimen merits careful re-examination, pending which it has been included in the key as "*C. octodentata* Balss non Haswell".

Distribution

From Amboina (Gordon 1941), Damar I. (Leene 1938), and Pulo Edam (de Man 1887*b*) to New Caledonia (A. Milne Edwards 1869) and Fiji (Balss 1938).

Previously recorded in Australia from Masthead I. (Grant and McCulloch 1906), North West I. (McNeill 1926), and Batt Reef, North I., Low Isles, and Masthead I. (Gordon 1941).

CAPHYRA ROTUNDIFRONS (A. Milne Edwards)

Figs. 1*H*, 2*J*, 3*A*–*C*, 3*K*; Plate 3, Fig. 4; Plate 5*J*

Camptonyx rotundifrons Milne Edwards, A., 1869, p. 156, pl. 7, figs. 11, 12.
Caphyra rotundifrons (A. Milne Edwards). Milne Edwards, A., 1873, p. 174. Borradaile, 1900, p. 579. Calman, 1900, p. 20. Nobili, 1901, p. 11 (key only, corrected Nobili 1906, p. 188). Doflein, 1904, pp. 95–6. Rathbun, 1907, p. 60, pl. 1, fig. 4; 1911, p. 204. McNeill, 1926, pp. 307–8. Gordon, 1941, p. 124, figs. 2*b*, 3*a*.
non *Caphyra rotundifrons* (A. Milne Edwards). Barnard, 1957, pp. 2–3, fig. 1 (= *Caphyra yookadai* Sakai, 1933).

Material Examined

11 ♂♂ (4–14 mm); 19 ♀♀ (8–24 mm). Ovigerous ♀♀ 9–15 mm from December and January.

QUEENSLAND: Murray I., North West I., Heron I. LORD HOWE I.: Elizabeth Reef.

Recorded habitats.—From green algae (*Chlorodesmis comosa* Bailey & Harvey) on reef flat.

Material illustrated.—Whole carapace, male abdomen, male pleopod, fifth leg: ♂ 14 mm, North West I., M. Ward (Aust. Mus. Reg. No. P12761). Front: Fig. 3*A*, ♀ 15 mm, Heron I., Dec. 1956, W. K. Patton; Fig. 3*B*, ♀ 12 mm, Heron I., 7.i.59, W.S.; Fig. 3*C*, ♀ 9 mm, Heron I., 7.i.59, W.S.

Description

Front.—Typically bilobed, the two smooth lobes being interrupted by a distinct median notch (see Figs. 3*A*, 3*B*). In a minority of specimens this notch is indistinguishable, the whole front forming a single smooth curve (see Fig. 3*C*).

Inner orbital lobes very ill developed, barely distinguishable from the front.

Anterolateral teeth.—Four, all very sharp and pointing forwards, decreasing in size from front to rear. In some specimens the fourth tooth is sufficiently small to be distinguished only with difficulty.

Carapace.—Relatively long, microscopically granular, especially on the anterior surface. Mesogastric ridges obscurely developed, epibranchials distinct, cervical grooves conspicuous.

Chelipeds.—With long hairs on the upper and outer surfaces. Anterior border of arm bearing two tubercles, and two large sharp teeth followed by a flat tooth near the articulation of the wrist. Under surface of arm smooth. The hand bears dorsally two carinae with a hollow between them. Neither carina bears spines, but in some specimens each ends anteriorly in a blunt tubercle.

The legs are relatively short for this genus and in undamaged specimens bear moderately long hairs.

Fifth leg.—Curved back dorsally over the carapace. The propodus less than twice as long as broad (1·7 times) and with bipinnate fringing hairs on both sides, those on the outer side being the longer, and those on the inner side increasing in stoutness distally and finally becoming bristles. Dactyl slightly shorter than propodus (0·93 times), very narrow (3·8 times as long as broad), proximally swollen, then gradually tapering overall, forming a conspicuous hook-like structure with short hairs on the inner side and elongate bipinnate hairs on the outer side. Distal two-fifths bare.

Male pleopod.—Short, practically untapered, and distinctly curved outwards at the tip. Beyond the basal lobes bare to the tip except for a group of bipinnate hairs a short way up on the inner side. This group continues distally for a little way as a row of short bristles. The terminal armature consists of a dense clump of long bristles on the inner side at the point where the tip is bent, and an irregular clump of 2–3 very long bipinnate bristles and numerous shorter ones. At the tip of the outer border these two clumps are connected on the lower surfaces by bands of bristles, and both clumps also extend to the upper surface.

Colour.—Translucent pea green, legs and chelae with darker green spots in indistinct longitudinal rows. The anterior fifth of the carapace bears transverse rows of darker green, the posterior four-fifths bears olive green longitudinal patches, often with white areas between them. Digestive glands and gonads show through the cuticle as brown and yellow respectively. Often one whitish mark in the posterior part of each mesobranchial area.

Comments

The authors have only obtained this species from a green alga, *Chlorodesmis comosa*, where it was discovered by Mr. W. K. Patton. In this weed it is abundant and shows marked protective coloration. In that the genus as a whole is believed to be commensal, this habitat may be unusual.

Distribution

New Caledonia, Samoa, Mauritius (Doflein 1904); Fiji (Balss 1938); Mariana Is. (Holthuis 1953); Torres Strait (Calman 1900).

CAPHYRA YOOKADAI Sakai

Figs. 1*I*, 2*K*, 3*H*; Plate 4, Fig. 1; Plate 5*K*

Caphyra yookadai Sakai, 1933, pp. 141–3, pl. xiii, fig. 3; 1936, p. 120, pl. xxxii, fig. 4; 1939, p. 378, pl. xliii, fig. 4.

Caphyra rotundifrons Barnard, 1957, pp. 2–3, fig. 1.

non *Caphyra rotundifrons* (Milne Edwards, A., 1869).

Material Examined

QUEENSLAND: ♂ 6 mm; ♀ 11 mm, "commensal with brown *Alcyonium* sp.", Myora, Moreton Bay, 28.vii.46, pres. J. S. Hynd (Aust. Mus. Reg. No. P12205).

Material illustrated.—Carapace, male abdomen, male pleopod: ♂ above. Fifth leg: ♀ above.

Description

This description is based on the present specimens, but with reference to Sakai's and Barnard's specimens.

Front.—Four-lobed, the median notch being distinct, but the lobes on each side almost confluent. (Barnard's specimens identified as *C. rotundifrons* are described as having "front straight or fully bilobed on either side of the median notch".)

Inner orbital lobes distinct and clearly separated (apparently obscurely so in two out of three of Barnard's specimens).

Anterolateral teeth.—The anterolateral margin forms a ledge which is obscurely divided into flattened lobes scarcely meriting the name of teeth. Four lobes are present except on the right side of the female specimen where a long first lobe apparently represents the fusion of two. (Sakai notes that only three teeth may be present. In Barnard's specimens the number of anterolateral teeth ranges from two to four.)

Carapace.—Very convex, broader than long, with the elevated central areas smooth and shining, and the margins, especially in the frontal area, bearing minute, regular granules. Mesogastric ridges faint in the female, distinct in the male; epibranchial ridges very clearly marked.

Chelipeds.—Short and granular, anterior border of arm without spines, under surface smooth; the wrist with 2 carinae running from the upper to the outer surface. Hand bears on the upper surface 2 elevated unarmed carinae separated by a broad depressed area. Movable finger flattened.

The legs are elongate and without hairs in the present specimens. (Barnard describes the legs as bearing plumose setae on their anterior surfaces, but these are not shown or described by Sakai.)

Fifth leg.—Only one fifth leg was present on the two specimens and this appeared to have lost some of its setae. Propodus 3·1 times as long as broad and with short fringing hairs along the length of the outer side, followed by a terminal clump. The inner side is bare except for a distal clump. Dactyl much shorter than the propodus (0·57 times), of moderate breadth (3·1 times), approximately lanceolate with a marked change in curvature on the inner side near the end. On the inner side there are a small number of subterminal hairs and suggestions of an almost continuous row (specimen damaged). On the outer side there is a short proximal row which probably extends further on an intact specimen. Barnard mentions plumose setae on the legs, but the present specimens have been subjected to too much handling for these to show.

Male pleopod.—Slightly curved, swollen just beyond the base and then almost untapered except at the tip. Beyond the basal lobes the inner surface of the swollen area bears sparsely arranged hairs followed by a very sparse row of fine bristles merging with the terminal armature. The outer side is bare except near the tip. The terminal armature consists of numerous bristles covering both upper and under surfaces and appearing in profile view on both inner and outer sides. They extend further back on the inner side than the outer, and *c.* 20 bristles are visible on this side and *c.* 12 on the outer side. The bristles on the inner side do not continue to the tip but leave a short terminal area.

Colour.—Present specimens colourless after prolonged preservation. Sakai describes the colour alive as follows: ". . . whitish pink, brown or white dots being visible under magnifying glass. Brown mottled speckles are on the upper and lower surface of the carapace in pairs: two are on protogastric regions and also a pair behind them on the median part; two are on each anterolateral margin, sometimes joined with each other, and a small one inside of them; two pair of light-coloured ones on the posterolateral margins and a small one inside of them; and a pair on the cardiac region, sometimes fused together. On the ventral side, a pair is on the suborbital region and one or two on the subhepatic region."

Comments

These specimens are identical with Sakai's description and differ from Barnard's only in that he described plumose setae on the legs. All specimens including the present ones have come from alcyonarians. Frequent examinations of the common brown "*Alcyonium*" in Moreton Bay have failed to add to Hynd's pair of specimens.

Distribution

Previously recorded from Izu and Kii Peninsulas, Japan (Sakai 1933, 1939) and South Africa (Barnard 1957).

CAPHYRA FULVA, sp. nov.

Figs. 1*J*, 2*L*, 3*I*; Plate 4, Fig. 2; Plate 5*L*

Material Examined

3 ♂♂; 2 ♀♀, Heron I., in fawn *Xenia*-like alcyonarian, 7.i.59, W.S. and N. Heather, designated as follows: holotype ♂ 9 mm, allotype ♀ 7 mm, paratypes ♀ 8 mm (ovigerous) and 2 ♂♂ 6 mm.

Material illustrated.—Holotype.

Description

Front.—Four-lobed, the median notch being distinct, but the lobes on each side almost confluent.

Inner orbital lobes small, clearly separated from the frontal lobes.

Anterolateral teeth.—Typically 4, sharp, with points directed anteriorly, decreasing in size from front to rear. On the allotype there are 5 teeth on the right side, the last 2 being very small; there are also 5 teeth on the left, of which the fourth is minute.

Carapace.—Microscopically punctate, sometimes bearing microscopic hairs, slightly broader than long and with the broadest point somewhat behind the last anterolateral teeth. Mesogastric and epibranchial ridges are present.

Chelipeds.—Microscopically granular. Anterior border of arm bears 3–5 spines increasing in size distally; the under surface in most specimens bears 5–6 sharp spines. The hand is rounded and without carinae except for a single one on the inner side of the upper surface. This bears a spine a third of the distance along, followed by a blunt distal tubercle.

The legs are elongate and slender with hairy dactyls.

Fifth legs.—Curved back over the dorsal surface. Propodus roughly twice as long as broad (1·8 times) and with long fringing hairs on both surfaces. Dactyl slightly shorter than propodus (0·85 times), 3·5 times as long as broad, with a sharp change in curvature just beyond the middle. Proximally with fringing hairs on both sides and distally bare.

Male pleopods.—Practically straight, tapering slightly to a narrow neck and terminating in a widely flared tip bearing a papilla on its upper surface. Beyond the basal lobes bare on the outer side up to the terminal armature; bare on the inner side for about three-fifths of its length, from whence there are sparsely scattered spinules which continue to the tip, becoming gradually larger. Terminal armature consists of sparsely arranged bristles on the upper side mostly as a single row near the edge of the flared area. There is a distal outer patch with *c*. 15 visible in profile view which continues to the under surface where a broad scattered band almost merges with the inner spinules. Just below the flare on the inner side there is a dense patch of stout recurved bristles, *c*. 12 in number, and just above them a second patch of normal bristles, *c*. 6 in number.

Colour.—Background colour pale cream with longitudinal reticulated areas of brown typically well developed. These areas comprise a small median mesogastric area, two broad submedian longitudinal bands, each extending to the hind end of the carapace and each with a discrete anterior branch leading to the orbit. In addition there is a short lateral area opposite each fourth anterolateral tooth.

Comments

The species is not at all common and is apparently restricted to a fawn-coloured *Xenia*-like soft coral. Its colour when alive merges against the background of its host, hence the specific name. It more readily quits the tentacle of this than in the case of *Caphyra laevis* living in blue-grey *Xenia*.

This species is clearly distinguished from *C. yookadai* by the carination of the dorsal surface of the cheliped. The row of spines on the under surface of the arm of the cheliped and the form of the first male pleopods are also diagnostic.

Possible Diphyletic Origin of Caphyra

Balss (1934, p. 506), after dismissing *C. archeri* Walker as being probably an oxyrhynchid rather than a portunid, considers that the remainder either derive from *Thalamonyx* ("ceux dont le bord frontal est bilobe") or from *Charybdis* ("ceux dont le bord frontal est simple").

The following comments seem appropriate:

(1) The distinction between a bilobed and non-bilobed front is an insecure one upon which to recommend a drastic division of the genus. Thus there is variation between a bilobed and an entire front within a single species, *C. rotundifrons* (see Figs. 3*A*–*C*).

(2) The majority of the species which have not bilobed fronts have either four-lobed, six-lobed, or six-toothed fronts as distinct from "simple".

(3) In a previous paper (Stephenson and Hudson 1957) the closeness of *Thalmonyx* to *Thalamita* was commented upon; and indeed they are probably best regarded as synonyms. Similarly *Thalamita* and *Charybdis* are most difficult to separate with five species of the former extremely close to one species of the latter.

(4) The structure of the male pleopods in the five species of *Caphyra* for which they have been described do give a hint of two subgeneric groups. Thus the three species *C. laevis*, *C. fulva*, and *C. polita* (see Gordon 1941, fig. 1*b*) have flared tips reminiscent of some species of *Thalamita* (e.g. *T. sexlobata* and *T. sima*, see Stephenson and Hudson, 1957, figs. 3*B*, 3*C*). The other two species, viz. *C. rotundifrons* and *C. yookadai* have non-flared pleopods somewhat reminiscent of those in *Charybdis* (see Stephenson, Hudson, and Campbell 1957, fig. 3). Until the pleopods of more species of *Caphyra* are known, any subdivision of the genus based upon their structure would be unwise. This is especially so since in general facies, including the nature of the front, each of the above groups is heterogeneous.

Subfamily **PORTUNINAE**, usus nov.

KEY TO THE INDO-PACIFIC GENERA OF SUBFAMILY PORTUNINAE

This differs from those in the literature and is based upon the most obvious of the features, i.e. the numbers of anterolateral teeth. "Small", "minute", and "rudimentary" teeth are included below, these being plainly visible if looked for. In three genera the numbers of teeth vary from species to species; thus *Lupocyclus* and *Portunus* which are typically nine-toothed may have fewer, and *Charybdis* which is typically six-toothed may have more. To allow for this these genera are duplicated or triplicated in the key. Specimens of *Portunus* with nine, eight, and six teeth are accommodated in the key. The very unusual specimens with other than these numbers of teeth are best identified by reference to the general facies of the species (see Stephenson and Campbell 1959).

1. 9 anterolateral teeth 2
   8 anterolateral teeth 5
   7 anterolateral teeth 7
   6 anterolateral teeth 8
   5 or fewer anterolateral teeth 11

2(1). Anterolateral teeth alternately large and small (carapace only a little broader than long) .... *Lupocyclus* Adams & White (1849)
   Anterolateral teeth subequal, or if smaller teeth present, these not alternating with larger ones 3

3(2). Carapace almost exactly as broad as long; basal antennal joint narrow, and with no distal lobule . . *Carupella* Lenz & Strunck (1914, p. 278) (not recorded from Australia)
   Carapace broader than long; basal antennal joint relatively broad, and with distal lobule 4

4(3). Hand of cheliped inflated and smooth; surface of carapace smooth, and regions ill defined .... *Scylla* de Haan (1833)
Hand of cheliped prismatic and costate; surface of carapace divided into regions .... *Portunus* Weber (1795, p. 93)

5(1). Last anterolateral tooth markedly larger than the remaining, which are subequal .... *Portunus* Weber (1795, p. 93) (certain spp. only, e.g. *P. longispinosus* (Dana) 1852*b*, p. 277, pl. 17)
Last anterolateral tooth not larger than most of the remainder 6

6(5). Carapace much broader than long (3 of the 8 teeth much smaller than the remainder) .... *Charybdis* subgenus *Goniosupradens* Leene (1938, pp. 18–19) (not recorded from Australia)
Carapace only slightly broader than long (large and small teeth alternating) .... *Lupocyclus* Adams & White (1849)

7(1). 6 large and 1 small anterolateral teeth .... *Charybdis* subgenus *Charybdis* de Haan (see Leene 1938, p. 18)
5 large and 2 very small anterolateral teeth .... *Charybdis* subgenus *Goniosupradens* Leene (1938, pp. 18–19) (not recorded from Australia)
4 large and 3 very small anterolateral teeth .... *Charybdis* subgenus *Gonioinfradens* Leene (1938, p. 18) (not recorded from Australia)

8(1). 6 anterolateral teeth subequal 9
Second anterolateral tooth much smaller than the remainder, which are subequal ..10
Last anterolateral tooth much larger than the remainder, which are subequal but irregularly spaced .... *Portunus* Weber (1795, p. 93) (Some spp. only, e.g. *P. macrophthalmus* Rathbun 1906, p. 871)

9(8). Chelae extremely long, arm distinctly longer than breadth of carapace .... *Lupocyclus* Adams & White (1849) (single sp. *L. philippinensis* Semper (1880, p. 68), not recorded from Australia)
Chelae of normal length, arm shorter than breadth of carapace .... *Charybdis* de Haan (1833, p. 10) (most spp., see Leene 1938)

10(9). Second anterolateral tooth small .... *Charybdis* de Haan (1833, p. 10) (one sp. only, *C. rathbuni* Leene (1938, p. 97–9, fig. 52), not recorded from Australia)
Second anterolateral tooth tiny .... *Thalamita* Latreille (1829, p. 33) (the "*exetastica*" group; see Stephenson and Hudson 1957, pp. 361–2)

11(1). Tips of chelipeds pointed, spines on hands of chelipeds normally developed 12
Tips of chelipeds spoon-shaped, spines on hands of chelipeds exceptionally well developed ..*Thalamitoides* A. Milne Edwards (1869, pp. 146–7) (not recorded from Australia)

12(11). Chelae extremely long, arm distinctly longer than breadth of carapace .... *Lupocyclus* Adams & White (1849) (single sp. *L. sexspinosus* Leene (1940, p. 176), not recorded from Australia)
Chelae of normal length, arm shorter than breadth of carapace .... *Thalamita* Latreille (1829, p. 33) (including *Thalamonyx* A. Milne Edwards 1873, p. 168; see Stephenson and Hudson 1957, p. 361)

Of the genera in the above key two (*Carupella* and *Thalamitoides*) have not been recorded from Australia, and three (*Thalamita*, *Charybdis*, and *Portunus*) have been dealt with in previous papers of this series (Stephenson and Hudson 1957; Stephenson, Hudson, and Campbell 1957; Stephenson and Campbell 1959). The remaining genera, *Lupocyclus* and *Scylla*, are treated below.

Genus LUPOCYCLUS Adams & White

Lupocyclus Adams & White, 1849, pp. 46–7. Milne Edwards, A., 1861, p. 387. Alcock, 1899, pp. 22–3 (synon.). Leene, 1938, p. 10. Sakai, 1939, p. 382. Leene, 1940, pp. 168–9.

Generic Description

This description follows Alcock (1899) and Leene (1940) with slight modification.

Carapace.—Slightly broader than long, convex; regions faintly indicated. Covered with a fine pile of hairs through which protrude granular transverse ridges or groups of granules of definite positions. Front prominent, cut into 4 or 6 teeth. Anterolateral borders moderately oblique and curved, and approximately equalling the posterolateral borders; 5 or 6 anterolateral teeth, sometimes with small or minute denticles in some or all of the interdental spaces, bringing the total number to 8 or 9.

Orbits.—Large, with distinct dorsal inclination; upper border with 2 incisions; inner angle of lower border dentiform.

Antennules.—Folding transversely.

Basal antennal joint.—About as long as broad, filling orbital hiatus; not quite firmly fixed; flagellum standing in the orbital hiatus.

Epistome.—Short, somewhat sunken.

Buccal cavern.—Somewhat broader than long; efferent branchial channels well defined.

Chelipeds.—Either long or very long, with squamiform markings; if very long, much longer than any of the legs. Slender, and with the hand more slender than the arm. Arm with spines; wrist with spines on inner and outer angles; hand with spines and costae; fingers long and slender.

Walking legs.—Slender.

Fifth leg.—Flattened; merus bearing a spine posteriorly.

Male abdomen.—Third to fifth segments fused.

Partial Revision of the Species of the Genus

In view of the fact that there is a recent monographic treatment of this genus (Leene 1940) some justification for the present reasonably extensive treatment is necessary.

Specimens in the collections of the Department of Zoology, University of Queensland, while close to Leene's description of *L. rotundatus* Adams & White, 1849, (Leene 1940, pp. 169–71, fig. 3, pl. i), disagree with it in the following particulars:

(1) Present specimens are rounder. They have a length/breadth ratio of 85/100 as against 75/100 in Leene's plate.

(2) They have no conspicuous groove separating the lateral frontal teeth from the inner supra-orbital lobes.

(3) They have a different ornamentation of the central carapace area. Thus, using the terminology of the last paper of the present series (Stephenson and Campbell 1959), in the present specimens there is a broad gap between the epibranchial and metagastric ridges, against a very narrow one in Leene's (1940) plate i. Also the anterior mesobranchial ridge is a granulated area lying almost on the line of prolongation of the epibranchial as against distinctly posterior to it. Further, the metagastrics lie quite transversely instead of forming a broad posteriorly directed V-shape.

(4) They have a differently shaped male abdomen, with a more rounded ultimate segment.

(5) They have different first pleopods in the males. Leene figured and described some 6 or 7 very large spines on the anterior (under) surface as against two such spines on the upper surface in the present specimens.

It is evident that the present specimens are different from Leene's. After a survey of the literature they were shown to belong to *L. rotundatus* Adams & White, 1849, non Leene. They agree with the original descriptions and plate excepting that Adams and White describe the front as being divided into five equal dentiform lobes. A. Milne Edwards (1861) has pointed out that this is almost certainly a simple numerical error.

By reference to the shape of the front, the carapace markings, and the length/breadth ratio of the carapace, Leene's figured specimen can be referred to *Goniosoma inaequale* Walker, 1887.

Prior to Walker, Miers (1884) had doubts about whether an Australian specimen differed specifically from *L. rotundatus*, and had noted most of the essential features of *L. inaequalis* although not giving it specific status. Subsequent to Walker, only Henderson (1893) has recognized *L. inaequalis* as a distinct species. Since 1893 the two species have been confused, and an attempt is made below to clarify the synonymy, mostly through consideration of length/breadth ratios. Only two records (Laurie 1906, pp. 411–2; Balss 1922, p. 113) cannot be referred to one or other of the species with reasonable certainty and these are omitted. The true *L. rotundatus* which is not included in Leene's (1940) work is redescribed from the present material.

KEY TO INDO-PACIFIC SPECIES OF GENUS LUPOCYCLUS

1. 6 subequal and equally prominent frontal teeth ....*L. quinquedentatus* Rathbun (1906, p. 869, pl. 12, fig. 7, text fig. 28) (not recorded from Australia)
   2 pairs of frontal teeth protruding well forward, if a third pair present, these much further back 2

2(1). 6–8 spines on anterior border of arm of cheliped, 6 main anterolateral teeth ....*L. philippinensis* Semper (1880, p. 68) (not recorded from Australia)
   5–6 spines on anterior border of arm, 5 main anterolateral teeth (or if 6, the second smaller than the third) 3

3(2). Epibranchial ridges on carapace indistinct .... *L. sexspinosus* Leene (1940, pp. 176–9, fig. 6, pl. iv) (not recorded from Australia)
   Epibranchial ridges on carapace distinct 4

4(3). Broad gap between epibranchial and metagastric ridges ....*L. rotundatus* Adams & White (1849)
   Epibranchial almost joining metagastric ridges ....*L. inaequalis* (Walker) (1887)

LUPOCYCLUS ROTUNDATUS Adams & White

Figs. 1*K*, 2*M*; Plate 4, Fig. 3; Plate 5*M*

Lupocyclus rotundatus Adams & White, 1849, p. 47, pl. xii, fig. 4. Milne Edwards, A., 1861, p. 387. De Man, 1883, p. 153. Miers, 1884, pp. 184, 234–5 (part only, ♀ Port Molle). Miers, 1886, p. 186 (part only). De Man 1887*a*, p. 718. Alcock, 1899, pp. 23–4 (part only—four smallest specimens). Gordon, 1938, pp. 175–6. Sakai, 1939, pp. 382–3, pl. lxxx, fig. 5.

Material Examined and Illustrated

QUEENSLAND: ♂ 39 mm, off Lookout Point, North Queensland, 17.iii.58, otter-trawled in 7 fm on mud bottom, N. Haysom, "*Challenge*" Prawn Survey (carapace, male abdomen illustrated). ♂ 33 mm, Princess Charlotte Bay, 7.iii.58, otter-trawled, 10 fm, mud and rubble, N. Haysom, "*Challenge*" prawn survey (male pleopod illustrated). The first specimen has been deposited in the Australian Museum and the second in the Queensland Museum.

Description

Front.—Protruding with 4 teeth, the laterals almost merging with the inner supra-orbital lobes. Median teeth rounded, laterals triangular with convex outer sides.

Anterolateral teeth.—Six (including outer supra-orbital lobe), all stout, with beaded granular edges and inclined forwards. The first the broadest, the third the next broadest, the second the smallest, and the remainder subequal. Between the third and the fourth and again between the fourth and fifth there are "small teeth", or "spinules" less than a quarter the length of the teeth proper, and also with beaded edges.

Carapace.—Slightly broader than long, length 85 per cent. of breadth. Bearing the following main granular areas (nomenclature after Stephenson and Campbell 1959): frontal region—a pair of patches extending to the frontal teeth; protogastrics—one group of granules on each side; a pair of mesogastric ridges interrupted in the midline and concave anteriorly; a pair of metagastrics; a pair of cardiacs each in the form of a rounded patch; a minute median postcardiac. There are three pairs of mesobranchials; a conspicuous epibranchial ridge; and scattered granules running medially from the anterolateral teeth, especially from the third, fourth, and fifth.

Chelipeds.—Elongate, $2\frac{3}{4}$ times length of carapace. Anterior border of arm bearing 5 spines which become larger distally; posterior border with 2 spines, one near and one at the distal end. Wrist with 2 spines. Hand with 3 spines and 6 granular carinae. Fingers grooved, and approximately the length of the palm.

First male pleopod.—Smoothly and regularly curving to a non-flared acute tip. Beyond the basal lobes on the outer side minute backwardly directed spinules begin about half-way up the appendage and continue to just behind the tip where they become denser and sufficiently large to be termed "spines". The inner side bare for two-thirds of the way up, then bearing sparsely distributed microscopic spines which continue until replaced by the subterminal armature. Subterminal armature on the outer side merging with the general spinulation; on the inner side some 4 or 5 backwardly directed spines are visible in profile view. Subterminally on the upper surface there are 2 stout blunt conical spines, these being nearer the inner than the outer surface. The patch of bristles which was visible in profile view on the inner surface passes round to the under surface, where some 20 backwardly directed spines are present.

Distribution

Balanbangan, Borneo (Adams and White 1849); seas of Amboina (de Man 1883); off Ceylon and Andamans (Alcock 1899), off E. coast of Malay Peninsula (Gordon 1938); Japan (Sakai 1939).

Previously known within Australia from a single specimen, Port Molle, Queensland (Miers 1884).

LUPOCYCLUS INAEQUALIS (Walker)

Goniosoma inaequale Walker, 1887, pp. 110, 116, pl. 8, fig. 4.

Lupocyclus inaequalis (Walker). Henderson, 1893, p. 378.

Lupocyclus rotundatus Miers, 1884, pp. 184, 234–5 (part only—♀ Friday I.); 1886, p. 186 (part only). Alcock, 1899, pp. 23–4 (part only—two largest specimens). Rathbun, 1911, p. 210. Shen, 1937, pp. 98–9, fig. 1. Leene, 1938, p. 11; 1940, pp. 169–71, fig. 3, pl. i.

Description

See Leene (1940). The distinctions between *L. rotundatus* and *L. inaequalis* have already been given.

Distribution

Singapore (Walker 1887; Shen 1937), Gulf of Martaban (Henderson 1893), off Ceylon and Andamans (Alcock 1899). Seychelles (Rathbun 1911), and East Indies (Leene 1938).

Recorded in Australia only from Friday I. (Miers 1884).

Genus SCYLLA de Haan

Scylla de Haan, 1833, p. 11. Milne Edwards, A., 1861, p. 347. Haswell, 1882*b*, pp. 78–9. Alcock, 1899, p. 27.

SCYLLA SERRATA (Forskål)

Fig. 2*N*; Plate 4, Fig. 4; Plates 5*N*, 6*C*

Cancer serratus Forskål, 1755, p. 90.

Cancer olivaceus Herbst, 1796, p. 157, pl. xxxviii, fig. 3.

Portunus tranquebaricus Fabricius, 1798, p. 366.

Scylla serrata (Forskål). De Haan, 1833, p. 44. Milne Edwards, A., 1861, p. 349. Miers, 1876, pp. 27–8. Haswell, 1882*b*, p. 79. Alcock, 1899, p. 27. Shen, 1932, pp. 36–8, figs. 4, 5 (male pleopod). Boone, 1934, pp. 70–2, pls. 25–30. Leene, 1938, pp. 14–15. Sakai, 1939, pp. 384–5, fig. 4. Estampador, 1949*a*, pp. 99–101, pl. 1, fig. 1. Barnard, 1950, pp. 160–1, figs. 31*b*, 31*c*. Serene, 1952, pp. 134–7, pl. i, fig. 3, pl. ii, figs. 3, *C*. Edmondson, 1954, pp. 234–5, figs. 10*b*, 11*a–c* (male pleopod). Chhapgar, 1957, pp. 416–7, pl. 5, figs. *a–c* (male pleopod).

Lupa tranquebarica (Fabricius). Milne Edwards, H., 1834, p. 448.

Lupa lobifrons Milne Edwards, H., 1834, p. 453.

Scylla tranquebarica var. *oceanica* Dana, 1852*b*, p. 270. Stimpson, 1907, p. 75.

Scylla oceanica Dana. Estampador, 1949*a*, pp. 101–2, pl. 1, fig. 2. Serene, 1952, pp. 134–7, pl. i, fig. 1, pl. ii, figs. 1, *A*.

Scylla tranquebarica (Fabricius). Estampador, 1949*a*, p. 103, pl. 3, fig. 1. Serene, 1952, pp. 134–7, pl. i, fig. 2, pl. ii, figs. 2, *B*.

Scylla serrata var. *paramamosain* Estampador, 1949*a*, p. 104, pl. 3, fig. 2. Serene, 1952, pp. 134–7, pl. i, fig. 4, pl. ii, figs. 4, *D*.

Discussion of Synonymy

Serene (1952) has noted that a complete synonymy would exceed 80 references, hence only selected ones are included above, stressing the more recent and more controversial.

Until the work of Estampador (1949*a*, 1949*b*) it had become generally accepted that there was only one species of *Scylla*, *S. serràta* (Forskål). In particular *S. tranquebarica* (Fabricius) with its variety *oceanica* Dana were regarded as synonyms.

Estampador considered that, in the Philippines, there are four sorts of *Scylla:*

(1) General colour deep ferrugineous brown ranging to light purplish brown with irregular small whitish spots on carapace and last legs. Setae on carapace restricted to hepatic region. H mark on carapace relatively faint. Usually living in holes. This was regarded as *S. serrata.*

(2) General colour predominantly green to greyish green. Carapace legs and abdomen with large pigmented areas of whitish grey bordered by purplish dark brown lines. Brush-like setae abundantly on carapace. H mark on carapace deeply impressed. "Prefers a nomadic life." This was regarded as *S. oceanica* (Dana).

(3) General colour deep purplish drab-green. Large pigmented areas only distinct on last legs and abdomen of female. Chelipeds enormously big. H mark on carapace deeply impressed. This was regarded as *S. tranquebarica* (Fabricius).

(4) As *S. serrata* but with the median frontal lobes slightly more anteriorly produced than the laterals. Outer of two spines at base of fingers smaller than inner but not obsolescent or dentiform. Colour lighter. Estampador described this form as a new variety of *S. serrata*, var. *paramamosain.*

He supported these separations by reference to variations in spermiogenesis and ookinesis; also to the form and physical constitution of the chromosomes. The cytological evidence of differences between the groups is not impressive.

Estampador noted that the Philippine fishermen recognize either two or three different groups; if the former, they designate a *mamosain* group without colour markings (*S. serrata* and the variety *paramamosain*) and a *banhawin* group with colour markings (*S. oceanica* and *S. tranquebarica*).

Serene (1952) notes that the Vietnam fishermen also recognize four groups which translate to: banana or white crabs, green crabs, rust red crabs, and moving ("roulant") crabs. Serene himself claims that two categories are tolerably easily separated on a basis of coloration, i.e. the rust and moving crabs (corresponding to Estampador's *mamosain* group) and the banana and green crabs (corresponding to Estampador's *banhawin* group). These Serene regards as species with the subdivisions of each as varieties. However, to avoid complications and recognizing the tentative nature of the work, he adopts Estampador's nomenclature.

After redescribing the fresh colours, and noting that they are useless features for use upon preserved material, he lists morphological features which separate the forms. He shows that the relative length of the chelipeds is not a good character, nor is the conspicuousness of the H groove on the carapace, nor is the relative protrusion of the median frontal lobes in *S. serrata* var. *paramamosain.*

The characters he found useful were:

(1) In males of similar size, length of external spine on upper surface of hand of cheliped, near the finger. This is very feebly developed in *S. serrata*, slightly developed in the var. *paramamosain*, and well developed in the other two forms.

(2) In males of similar size length of spine on antero-inferior border of the carpus. This is absent in *S. serrata*, feebly developed in *S. oceanica*, moderately developed in *S. tranquebarica*, and well developed in *S. serrata* var. *paramamosain*.

(3) Frontal lobes more acute in *S. oceanica* and more rounded in *S. serrata*, with the others intermediate.

(4) Relatively broader posterior border of carapace in *S. oceanica*.

(5) Relatively narrower orbital space in *S. oceanica*.

(6) Relatively acuter but shorter anterolateral teeth in *S. oceanica*.

Comparing the work of Estampador and Serene, it will be noted that they agree in separating two groups, marked from unmarked crabs, and further agree that each group can be divided into two on the basis of colour. Broadly speaking they disagree upon the features other than colour which can be used to effect a separation.

All the live specimens seen by the authors from central and southern Queensland and from New South Wales, are unmarked and thus belong to *S. serrata* or its var. *paramamosain*. The more important differences between these two (viz. spines on hand and wrist of chelipeds) could well be due to different degrees of wear, which would be related to different intervals since the last moult. Until this possibility has been eliminated, it seems preferable not to recognize the var. *paramamosain*.

Conspicuously mottled crabs have been reported by the general public from islands within the Great Barrier Reef, from Cairns and northwards, but the authors have not seen these alive. One specimen (♂ 27 mm, Aust. Mus. Reg. No. P4285) from Finches Bay, Cooktown, might have been one of the mottled forms. On morphological features it may possibly be Serene's *S. tranquebarica*, although the distinctions from *S. serrata* var. *paramamosain* are extremely slight.

It is felt that a great deal more work is required before the separation of the old *S. serrata* into four forms can be regarded as justified. In particular evidence is required upon:

(1) The effect of wear and tear upon the spinulation of the chelae and shape of the anterolateral teeth.

(2) The effect of the general environmental background upon the basal colour and the markings of individuals.

(3) Whether given individuals live permanently in one type of habitat (e.g. holes amongst mangrove roots) or whether they migrate.

(4) The structure of the male pleopods. These structures, which are of great diagnostic value, were not considered by either Estampador or Serene.

Therefore, and tentatively, the four forms of Estampador and of Serene are fused into the synonymy.

Material Examined

14 ♂♂ (23–190 mm); 10 ♀♀ (19–165 mm).

QUEENSLAND: Cape York, Flinders I., Cooktown, Townsville, Bloomfield R., Mackay, Gladstone, Burnett R., Caboolture R., Caloundra, Brisbane R., Clontarf, Southport. NEW SOUTH WALES: Port Jackson, Sailor's Bay, Middle Harbour, Sydney. WESTERN AUSTRALIA: Broome. NORTHERN TERRITORY: Darwin.

Recorded habitats.—Mangrove mud flats, burrows on bank, M.T.L.

In addition a considerable number of specimens from central and southern Queensland and from northern New South Wales have been examined cursorily.

Material illustrated.—Carapace, male abdomen: ♂ 190 mm, Caboolture, March 1952, pres. Dept. Harb. and Mar. (Zool. Dept. Univ. Qld.). Male pleopod: whole mount ♂ 140 mm, Cooktown, D. Chapman (Zool. Dept. Univ. Qld.), tip ♂ 67 mm (Qld. Mus.).

Description

General.—Considered unnecessary.

Male pleopod.—Rather long, sinuous, and evenly tapered to a blunt tip. Beyond the basal lobes on the outer side a band of hairs commences on the upper surface. These extend distally to form a broad band of spinules which extend on the upper outer surface towards the tip and also spread to the under surface covering it almost entirely from about half-way up the appendage and becoming sparser towards the tip. On the inner side a dense patch of hairs on the basal area extends up the appendage as a band of short fine hairs. These become much sparser and shorter towards the tip and continue as a row of small spinules on the inner border. In larger specimens the finer hairs on the upper surface may be absent so that only a row on the inner border remains.

Comments

The smallest specimen seen (Aust. Mus. Reg. No. P3827, ♂(?) 13 mm, doubtfully Australian) looks superficially quite atypical because of the fine pile of hairs over most of the carapace.

This species, known locally as the "mud crab", is the largest of the Australian portunids in terms of bulk and is greatly sought after as food. Catching methods include: (1) probing in burrows, typically amongst mangroves, with a long iron hook, (2) in shallow baited nets ("dilly nets") hung down vertically from boats or piers, (3) in baited pots, and (4) in tangle nets. From the fact that sometimes burrow-probing, and on other occasions trapping methods, give the best results, it seems probable that the population has an alternation between sedentary and mobile phases in the life cycle. Mr. E. M. Grant (personal communication) reports that individuals may rise to the surface at night and swim purposefully.

The general habitat of the species in the region from central Queensland to northern New South Wales is in muddy estuaries which are typically lined with mangroves. It occurs in Moreton Bay down to 4 fm, and penetrates upstream into water of very low salinity. After freshwater floods, unusual concentrations of mud crabs have been reported off the mouths of rivers, and it is generally believed that they have been swept downstream.

Distribution

Throughout the Indo-West-Pacific from E. Africa and the Red Sea to Japan, Tahiti and New Zealand (Chhapgar 1957).

Previous Australian records are: "Neu Holland" (Hess 1865), Queensland (Yonge 1930; Stephenson *et al.* 1931; Roughley 1936; Dakin, Bennett, and Pope 1952), New South Wales (Stead 1898) and Western Australia (subfossil) (Etheridge and McCulloch 1916).

Subfamily **PODOPHTHALMINAE** Borradaile, 1907

Only one genus has been recorded from the Indo-West-Pacific.

Genus PODOPHTHALMUS Lamarck

Podophthalmus Lamarck, 1801, p. 152. Alcock, 1899, p. 92 (early lit.). Sakai, 1939, pp. 426–7.

Key to the Indo-West-Pacific Species of Genus Podophthalmus

Carapace broad (breadth *c.* 2·5 times length); front entire, deflexed; supra-orbital borders inclined; distal portion of inner surface of palm bearing a spinule . . *P. vigil* (Fabricius) (1798)

Carapace breadth *c.* 2 times length; front bilobed, horizontal; supra-orbital borders transverse; distal portion of inner surface of palm without a spinule .... *P. nacreus* Alcock (1899, pp. 93–4) (not recorded from Australia)

Podophthalmus vigil (Fabricius)

Figs. 1*L*, 2*O*; Plate 5, Fig. 1; Plate 5*O*

Portunus vigil Fabricius, 1798, p. 368.

Podophthalmus spinosus Lamarck, 1801, p. 152; 1838, p. 471.

Podophthalmus vigil (Fabricius). Leach, 1815, p. 149, pl. 108; Milne Edwards, A., 1861, p. 420. Boone, 1934, pp. 81–5, pls. 37, 38. Shen, 1937, p. 137, fig. 20. Leene, 1938, pp. 12–13 (lit. and synon.). Sakai, 1939, p. 427, pl. xlviii. Stephensen, 1945, p. 137, figs. 32*a,b* (male pleopods). Edmondson, 1954, pp. 271–2, figs. 43*d,e*, 44.

Material Examined

19 ♂♂ (55–142 mm); 8 ♀♀ (76–117 mm).

QUEENSLAND: Moreton Bay (Bribie I., Pearl Banks, Woody Pt., Peel I., Victoria Pt., Stradbroke I.), Southport, Morris I. (Claremont Group). WESTERN AUSTRALIA: Exmouth Gulf.

Recorded habitats.—Trawled, 5–10 fm, sandy mud and weed.

Material illustrated.—♂ 92 mm, east channel Pearl Banks, Moreton Bay, trawled on soft mud 12 m, coll. E. Grant, 23.v.52 (Zool. Dept. Univ. Qld.).

Description

General.—Considered unnecessary.

Male pleopod.—The broad base curves slightly to a long neck which tapers to a fine extended tip. A row of stout, short, tubercle-like spines commences about half-way up the appendage on the outer side. This row extends to the tip, the spines becoming progressively smaller and sharper and merging with the terminal armature. This consists of sparsely arranged recurved spines which form irregular upper, under, and inner rows extending a short distance back from the tip and with from 5–7 spines per row.

Distribution

Previously recorded in Australia from Brisbane R. (subfossil) (Etheridge and McCulloch 1916) and Southport (Boone 1934). Now also from Western Australia.

Outside Australia from the Indian Ocean, Red Sea (Shen 1937) and Iranian Gulf (Stephensen 1945) through Formosa and the Philippines (Balss 1922) to Hawaii (Shen 1937; Edmondson 1954).

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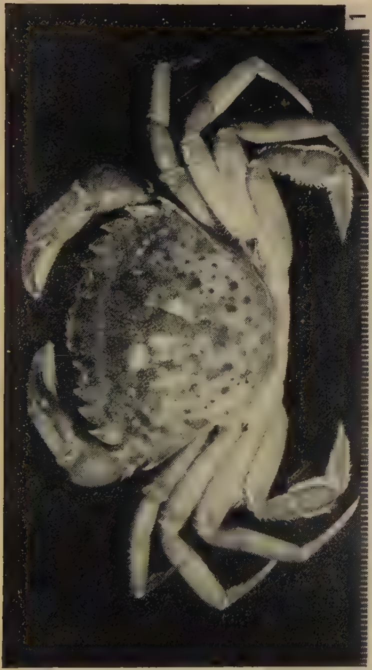
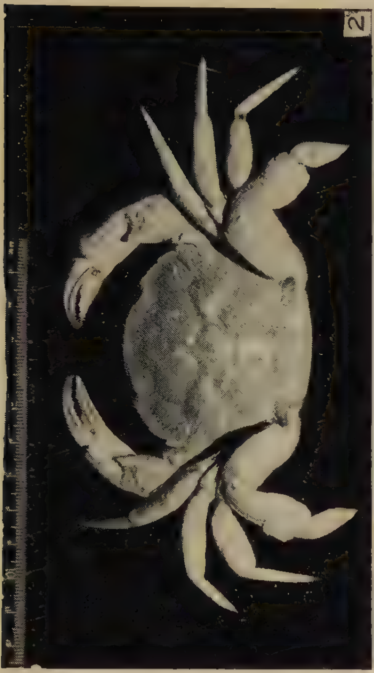
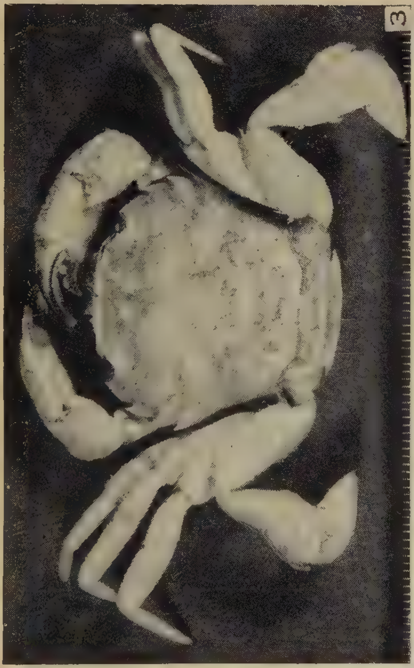
AUSTRALIAN PORTUNIDS. IV







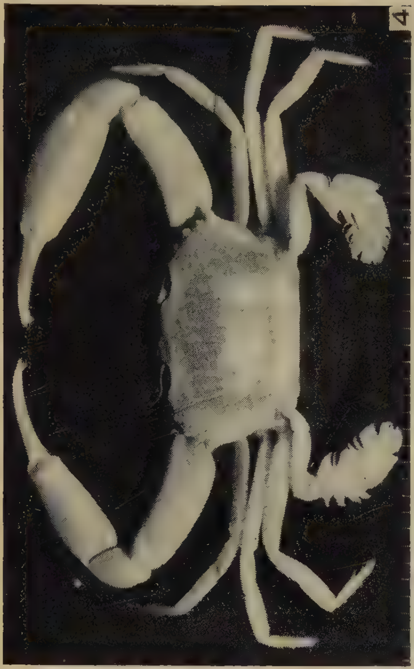
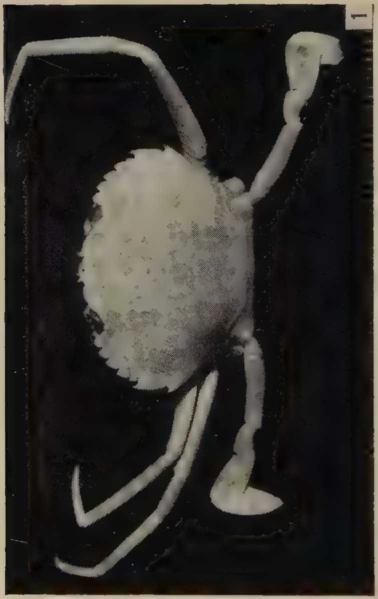
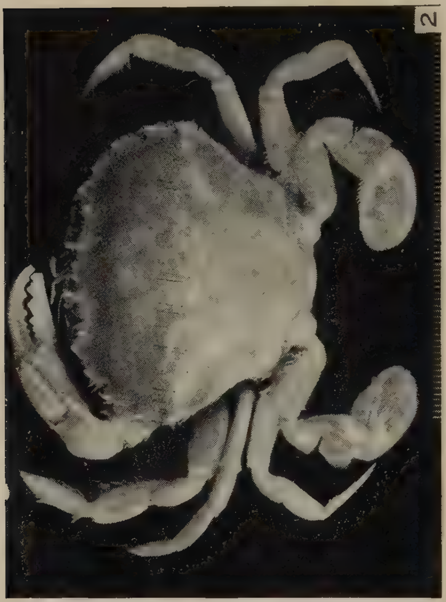
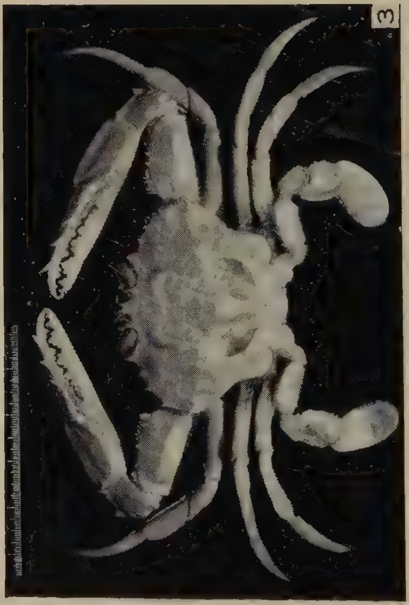


Fig. 1.—*Carcinus maenas.* Fig. 2.—*Nectocarcinus integrifrons.* Fig. 3.—*N. tuberculosus.* Fig. 4.—*Libystes paucidentatus.*
Scale divisions 1 mm.

AUSTRALIAN PORTUNIDS. IV







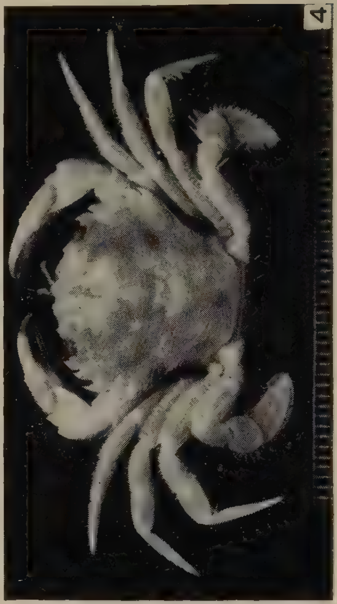
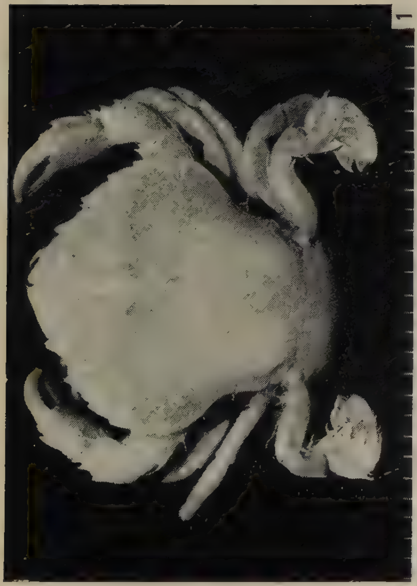


Fig. 1.—*Carupa tenuipes.* Fig. 2.—*Ovalipes punctatus.* Fig. 3.—*O. molleri.* Fig. 4.—*Macropipus corrugatus.* Scale divisions 1 mm.

AUSTRALIAN PORTUNIDS. IV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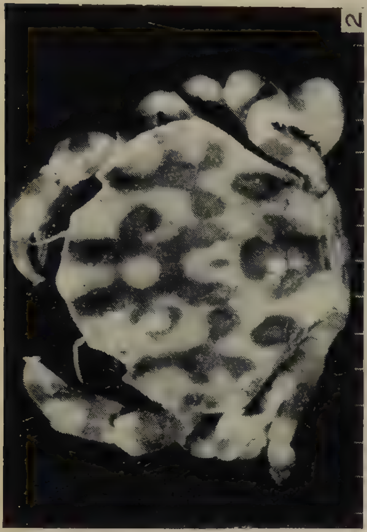
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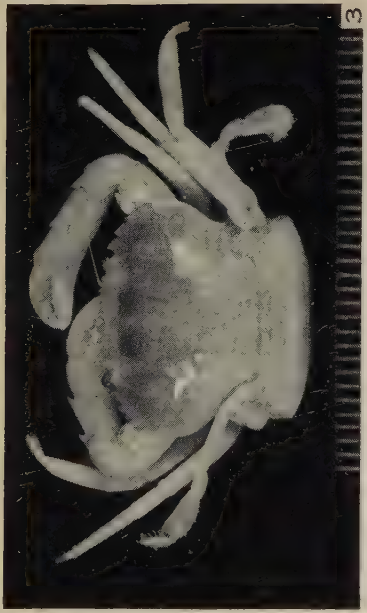
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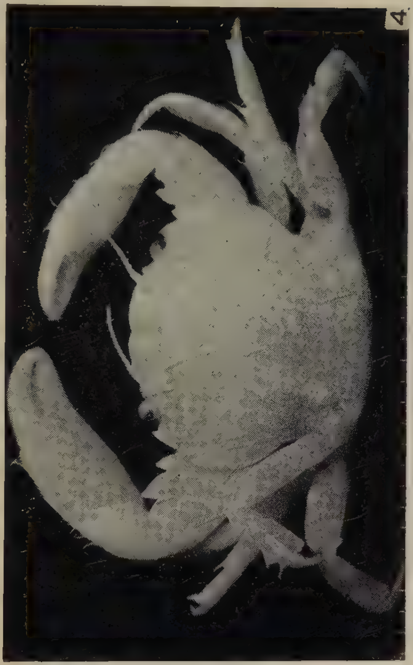
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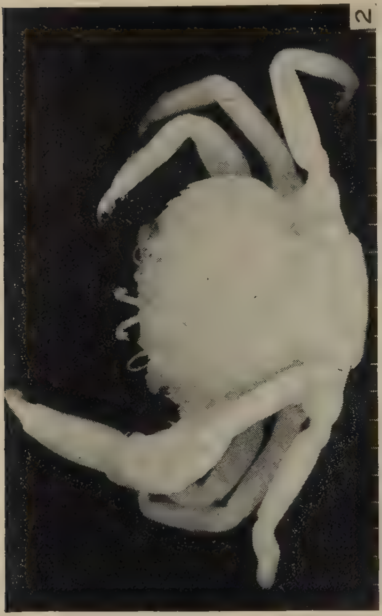
Fig. 1.—*Lissocarcinus polybioides.* Fig. 2.—*L. orbicularis.* Fig. 3.—*Caphyra laevis.* Fig. 4.—*C. rotundifrons.* Scale divisions 1 mm.

AUSTRALIAN PORTUNIDS. IV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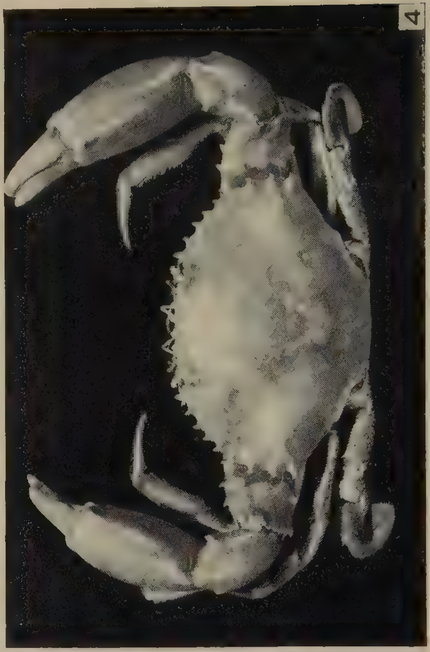
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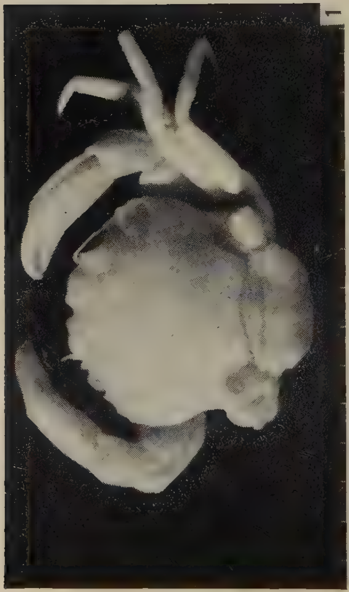
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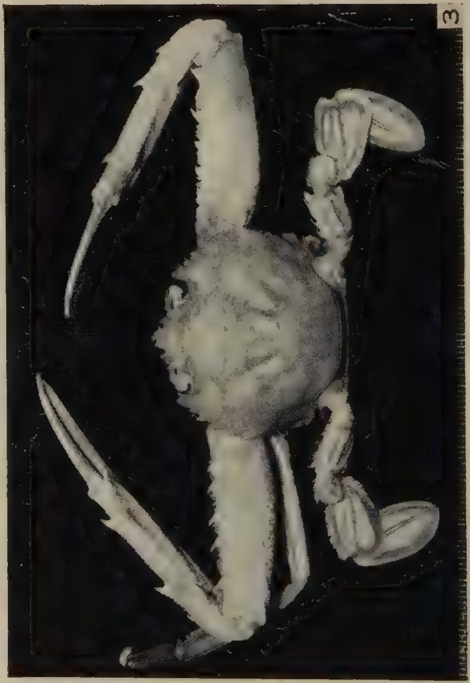
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Fig. 1.—*Caphyra yookadai.* Fig. 2.—*C. fulva.* Fig. 3.—*Lupocyclus rotundatus.* Fig. 4.—*Scylla serrata.* Scale divisions 1 mm.

AUSTRALIAN PORTUNIDS. IV

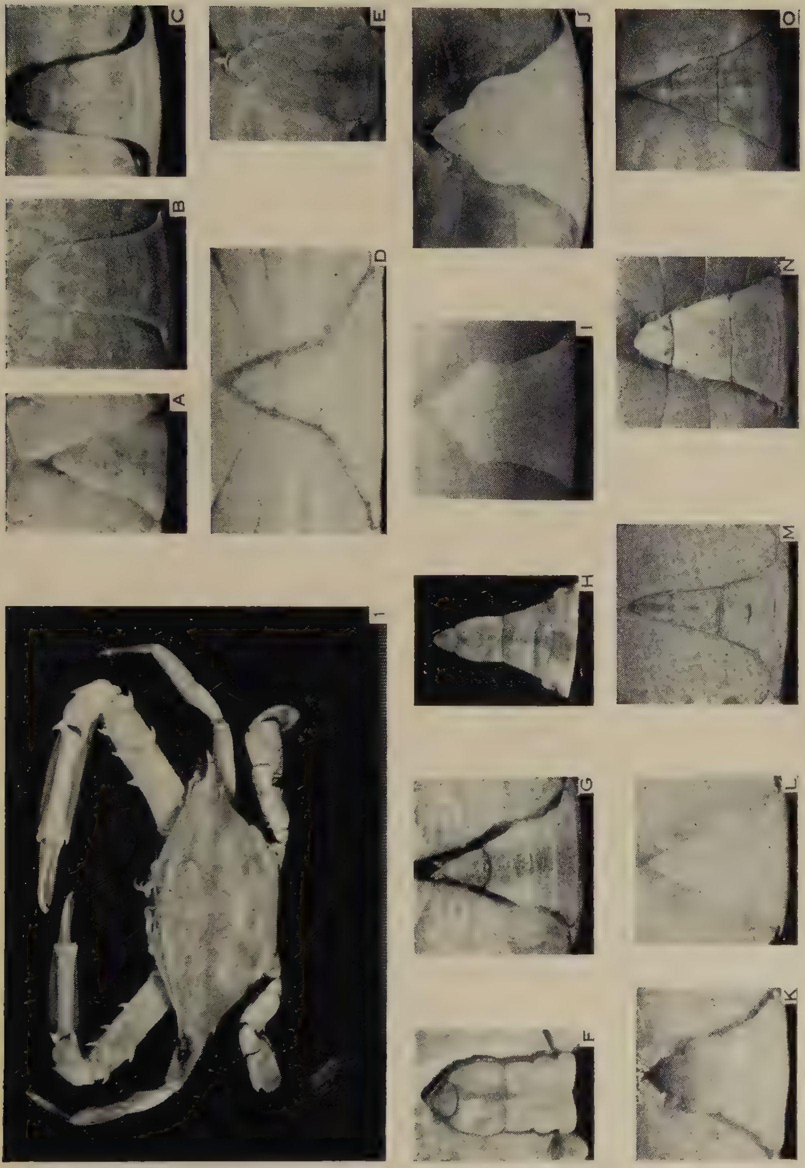
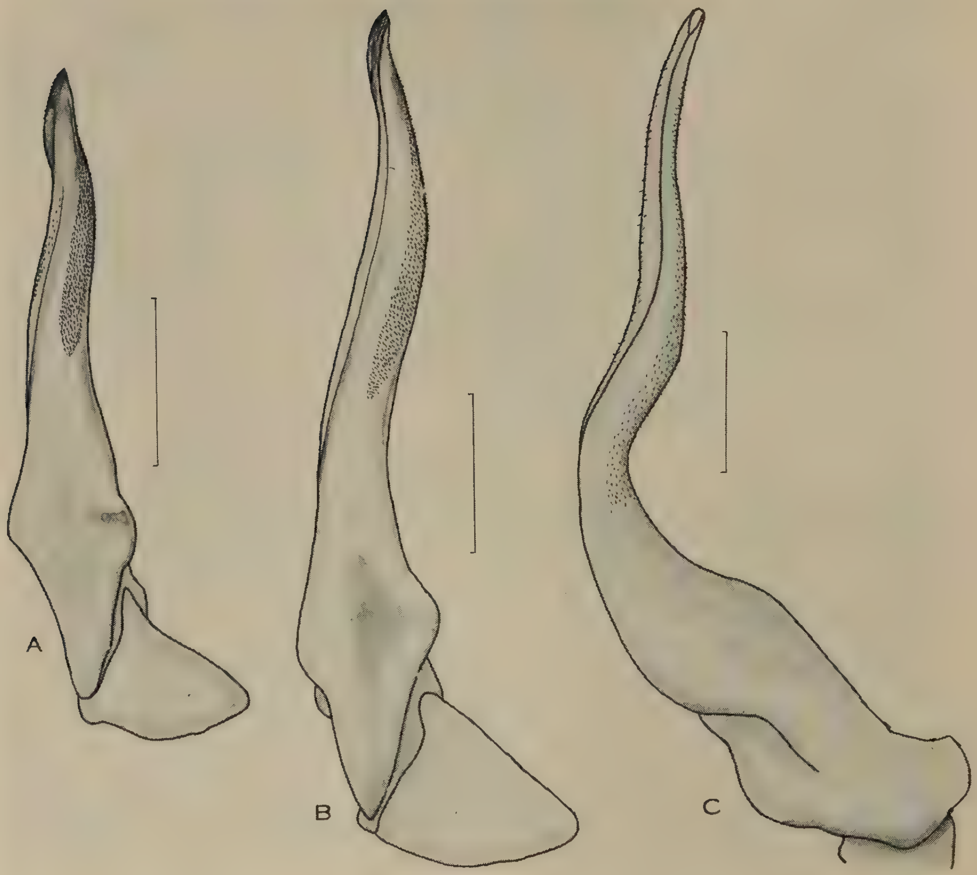


Fig. 1. *Podophthalmus vigil*. Scale divisions 1 mm. Figs. *A–O*.– Male abdomens. *A*, *Carcinus maenas*; *B*, *Nectocarcinus integrifrons*; *C*, *N. tuberculosus*; *D*, *Libystes paucidentatus*; *E*, *Ovalipes punctatus*; *F*, *O. molleri*; *G*, *Macropipus corrugatus*; *H*, *Lissocarcinus polybioides*; *I*, *Caphyra laevis*; *J*, *C. rotundifrons*; *K*, *C. yookadai*; *L*, *C. fulva*; *M*, *Lupocyclus rotundatus*; *N*, *Scylla serrata*; *O*, *Podophthalmus vigil*.



Wash drawings of male pleopods. *A*, *Nectocarcinus integrifrons*; *B*, *N. tuberculosus*; *C*, *Scylla serrata*. Scale lines 5 mm.

SUPPLEMENTARY DATA ON FRESHWATER MUSSELS (MOLLUSCA: PELECYPODA) OF THE AUSTRALIAN REGION

By I. D. Hiscock*

[*Manuscript received August* 4, 1959]

Summary

The holotype of *Unio moretonicus* Reeve has been found and identified as the Tasmanian *Velesunio*, which, on the grounds of priority, must become *V. moretonicus*; a lectotype has been selected for *Unio aucklandicus* Gray, and a number of dimensions of type specimens have been recorded.

I. Introduction

McMichael and Hiscock (1958) attempted to discuss all of the named freshwater mussels from Australasia and to assess their taxonomic status. In most cases the authors were able to examine the types, or photographs of types, of the named forms and to publish photographs of them. Where only syntypes existed, lectotypes were selected. In a few cases type material could not be located and such cases were treated variously.

A recent detailed examination of the collection of Australasian freshwater mussels in the British Museum (Natural History) has enabled some corrections and additions to be made. One "missing" holotype has been found and identified, resulting in a name change for the Tasmanian velesunionine mussel, a lectotype has been selected for the New Zealand *Unio aucklandicus* Gray (= *Hyridella* (*H.*) *aucklandica* (Gray)), and a number of dimensions and registration numbers, not available previously, have been obtained. These several findings are reported in detail below. The abbreviations used are as in McMichael and Hiscock (1958).

II. Taxonomy

Family **MUTELIDAE** Gray

Subfamily **VELESUNIONINAE** Iredale

Velesunio moretonicus (Reeve), comb. nov.

Plate 1, Figs. 1–5

Unio depressus Reeve, 1864, pl. xviii, sp. and fig. 81. (Non *Unio depressus* Lamarck, 1819.)
Unio moretonicus Reeve, 1865, pl. xxiv, sp. and fig. 118.
Unio legrandi Petterd, 1889, pp. 81–2.
Velesunio shuttleworthi (Kuster). Iredale, 1934, pp. 60–1, pl. iii, fig. 5, pl. iv, fig. 5.
Velesunio legrandi (Petterd). McMichael and Hiscock, 1958, pp. 395–8, pl. 2, figs. 6 and 7.

Remarks

McMichael and Hiscock (1958) discussed the nomenclatural confusion of the Tasmanian *Velesunio* and used the name *legrandi* Petterd, 1889, for it, on the grounds of the exactness of identity of *U. legrandi* compared with, in the absence of their holotypes, the uncertainty of either *U. shuttleworthi* Kuster, 1855, or *U. moretonicus* Reeve, 1865, both of which *may* have been Tasmanian shells and both of which are prior names.

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The holotype of *U. moretonicus* Reeve has now been located in the British Museum and, since it is, in fact, a Tasmanian shell and a *Velesunio*, the name *moretonicus* Reeve will replace *legrandi* Petterd for the Tasmanian velesunionine mussels.

The type specimen is a complete shell, previously unregistered. The left valve is labelled internally "Moreton Bay Mr. Strange H. Cuming". The tablet to which it is attached bears the following inscriptions: on the front face "*australis* var = *moretonicus* Sowerby. Moreton Bay"; on the back "*U. moretonicus* Sowerby Conch. Icon. fig. 118 type M.C.". The shell is undoubtedly the one used for Reeve's figure.

The original type locality was given as "Tasmania and Moreton Bay, Australia", but the shell is definitely Tasmanian.

The shell morphology of this specimen is typical of the velesunionine mussels of the Tamar River system, Tasmania, with the hinge rather weak and the BHI high. It is now registered, BM Reg. No. 1958–5–16–1.

The shell figured by Reeve (1864) as *Unio depressus* is now registered, BM Reg. No. 1958–5–16–2.

Dimensions (all lengths in mm)

Specimens	L	BL	BLI	MH	MHI	BH	BHI	W
U. moretonicus								
Holotype	72	22	31%	43	60%	39	90%	29
U. depressus Reeve	78	28	36%	49	63%	44	90%	28

Additional Registration; Dimensions

U. vittatus Lea, 1859 (McMichael and Hiscock 1958, p. 392): Holotype BM Reg. No. 1958–4–3–1.

U. evansi A. Adams & Angas, 1864 (McMichael and Hiscock 1958, p. 394): width of holotype 22 mm.

U. (*Alasmodon*) *stuarti* A. Adams & Angas, 1864 (McMichael and Hiscock 1958, p. 400): width of holotype 22 mm.

U. angasi Sowerby, 1867 (McMichael and Hiscock 1958, p. 404): width of holotype 24 mm.

U. shuttleworthi Lea, 1856 (Sowerby's 1866 figure) (McMichael and Hiscock 1958, p. 416): width of specimen 37 mm.

C. angasi subjecta Iredale, 1934 (McMichael and Hiscock 1958, p. 428): width of lectotype 20 mm.

Subfamily **LORTIELLINAE** Iredale

LORTIELLA RUGATA (Sowerby)

The lectotype of *Mycetopus rugatus* Sowerby, 1868, BM Reg. No. 44–1–12–160, is a complete shell, not an unmatched pair of valves as reported by McMichael and Hiscock (1958). The width of the shell is 21 mm. The mean width of the six paratypes is 23 mm.

Subfamily **HYRIDELLINAE** Iredale

HYRIDELLA (HYRIDELLA) AUCKLANDICA (Gray)

Plate 1, Figs. 6–10

Remarks

The exact identity of *Unio aucklandicus* Gray, 1843, seemed to be certain when Dell (1953, pl. 17, figs. 5 and 6, pl. 19, figs. 2 and 3) published photographs, which he had received from the British Museum, of its "type". McMichael and Hiscock (1958, pl. 12, figs. 13 and 14) published figures from the same negatives, but noted that this "type" consisted of unmatched valves. They also listed its registration number, BM Reg. No. 1951–9–6–17.

A recent examination of this specimen has shown that an earlier registration exists. The right valve bears, in small and faint writing, the number 42–11–9–76; on the left valve the number 76 is visible. Presumably these numbers had escaped notice when the specimen was registered in 1951.

The original number appears in the Register, with the entry "*Unio aucklandica*, Auckland. Presented by Dr. Sinclair R.N.". In addition, however, are numbers 42–11–9–75 to 82, all entered as "*U. aucklandica* Presented by Dr. Sinclair R.N.". This series of eight specimens must be the type series, but nowhere is there an indication that 42–11–9–76 is the holotype. Of the eight specimens, six have been located. These are:

42–11–9–75	left valve labelled* "Aukland *U. auklandica*" (*sic*). The right valve bears the number 42–11–*5*–75, but the *5* must be a curating error;
42–11–9–76	the unmatched valves, discussed above;
42–11–9–77	left valve labelled "Bay of Islands";
42–11–9–78	damaged, both valves labelled "Bay of Islands";
42–11–9–82	a juvenile, no writing on the shell;
42–11–9– ?	no number visible, right valve labelled "Bay of Islands".

Of these six specimens, numbers 75 to 77 are the form recognized by McMichael and Hiscock (1958) as *aucklandicus*, but 78, 82 and the unlabelled one are *Hyridella* (*Echyridella*) *menziesi* (Gray). Fortunately, despite this further confusion, the true identity of *aucklandicus* Gray can be determined. Gray's description of the species (1843, p. 257) includes ". . . inner surface pearly, purplish near the umbo, greenish on the hind edge". This part of the description can apply only to specimen 75, the left valve of which has a pronounced greenish area posteriorly, distal to the pallial line (see Plate 1, Fig. 8, where the area shows as a dark stain), a feature unique among the type specimens.

Specimen 42–11–9–75 is selected, therefore, as lectotype. Though specimen 76 has been figured twice as the "type", and is indeed *aucklandicus*, the fact that it is not a complete shell weakens its claim to selection.

The type locality, Auckland, as restricted by McMichael and Hiscock (1958) is unaltered.

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* Mr. S. P. Dance thinks that the handwriting on this shell, and on the others in this series, is probably Gray's own.

Dimensions (all lengths in mm)

Specimens	L	BL	BLI	MH	MHI	BH	BHI	W
U. aucklandicus								
Lectotype	78	16	21%	37	47%	33	89%	21
Specimen 42–11–9–76*								
Left valve	76	16	21%	38	50%	33	87%	—
Right valve	75	20	27%	36	48%	31	86%	—
Specimen 42–11–9–77	64	18	28%	34	53%	29	85%	18

* The dimensions given by McMichael and Hiscock (1958), measured from photographs, were incorrect.

Additional Registration; Dimension

U. menziesi Gray, 1843 (McMichael and Hiscock, p. 464): width of holotype 14 mm.

III. ACKNOWLEDGMENTS

The author wishes to thank the Trustees of the British Museum (Natural History) for permission to examine the collections, for providing the photographs of the shells in Plate 1 and for permission to publish them. He is most grateful to Mr. S. P. Dance of the Mollusca Section, Zoology Department, British Museum, for his assistance in the location of type material and for his helpful discussions.

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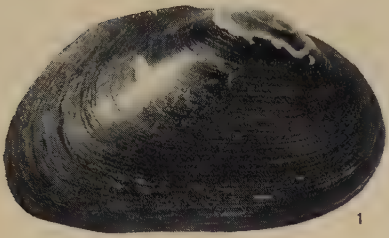
EXPLANATION OF PLATE 1

Figs. 1–5.—*Unio moretonicus* Reeve: Holotype.
Figs. 6–10.—*Unio aucklandicus* Gray: Lectotype.
(Photographs not to same scale; see text for dimensions.)

SUPPLEMENTARY DATA ON FRESHWATER MUSSELS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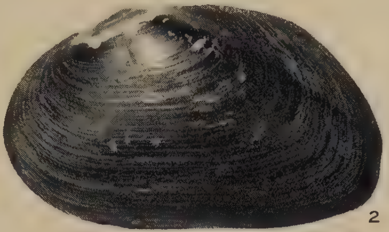
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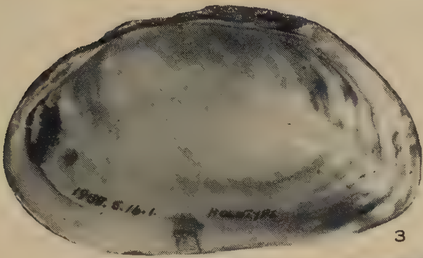

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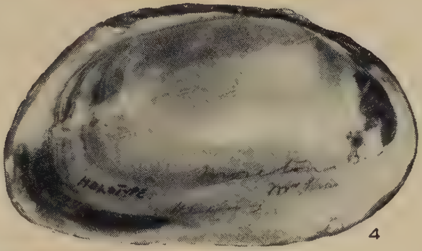

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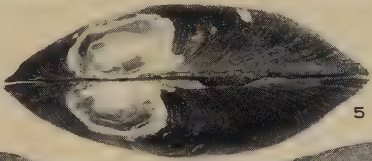
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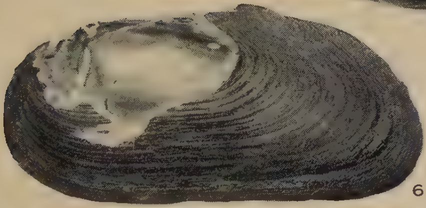
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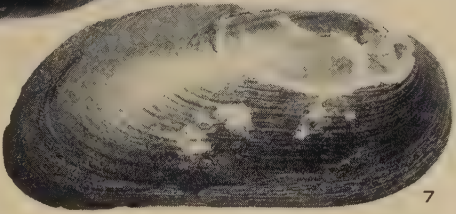
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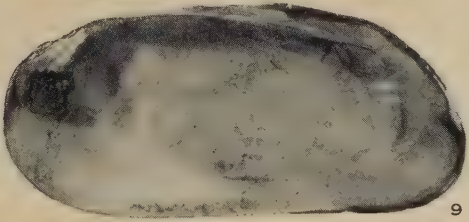
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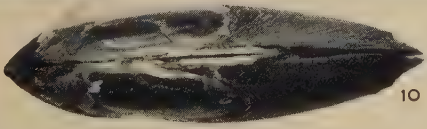
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THE INTERMEDIATE DEPTH WATERS OF THE TASMAN AND CORAL SEAS

I. THE 27·20 σ_t SURFACE

By D. J. Rochford*

[*Manuscript received February* 19, 1960]

Summary

The distribution of salinity, dissolved oxygen, and phosphates on the 27·20 σ_t surface of the Tasman and Coral Seas is examined. Their distribution patterns and the relations of salinity and phosphate values on this σ_t surface are explained by the horizontal mixing of three water types. These originate, one at the Antarctic Convergence, one in the western equatorial region of the Pacific, and one in the south-west Pacific. From the distribution of these water types and the topography of the 27·20 σ_t surface, general features of the intermediate depth circulation of the Tasman and Coral Seas are deduced.

I. Introduction

The characteristics of the primary external water masses entering the Tasman and Coral Seas at or near the surface have already been detailed (Rochford 1959), and their circulation has been inferred. Certain features of the deep circulation of these waters have also been described (Rochford 1960). In this and in a subsequent paper the characteristics and circulation of the intermediate depth waters are investigated. This paper deals with the waters on the 27·20 σ_t surface within the 700–1200 m stratum.

II. Materials and Methods

Table 1 lists the sources of the data and Figure 1 shows the location and the quarter of the year in which the data used in Section III were collected. The sources of additional data used in Section IV(*c*) are listed in Table 2.

All phosphate data have been corrected to a common salt error (×1·10, Wattenberg 1937) before use in this paper. In intermediate depth waters total phosphorus is almost entirely in the inorganic form and in this paper both values have been grouped together and termed phosphates.

III. 27·20 σ_t Surface

(*a*) *Selection of this Surface*

The 27·20 σ_t surface was chosen as the level on which the major part of the isentropic flow and horizontal mixing of the Antarctic Intermediate waters occurred in the Tasman and Coral Seas. Accepting the salinity minimum as the core of the Antarctic Intermediate waters, Figure 2 shows that, with the exception of the *Albatross* station at the equator, this σ_t surface coincided with the core of these Intermediate waters at all latitudes. Even in the case of the *Albatross*

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station there was a maximum difference in depth of only 100 m and in salinity of about 0·01‰ between the core of these waters and the 27·20 σ_t surface.

Table 1

SOURCES OF DATA USED IN SECTION III

Vessel	Month and Year	Reference
Albatross	Dec. 1947	Bruneau, Jerlov, and Koczy (1953)
Challenger	July 1951	Great Britain, Admiralty (1953)
Dana	Nov. 1928–Feb. 1929	Carlsberg Foundation, Copenhagen (1937)
Daifuji-Maru	July 1956	Shizuoka Prefectural Fisheries Experimental Station (1957)
Derwent Hunter	1952	C.S.I.R.O. Aust. (1953)
Derwent Hunter	1953	C.S.I.R.O. Aust. (1954)
Derwent Hunter	1954	C.S.I.R.O. Aust. (1956)
Derwent Hunter	1955	C.S.I.R.O. Aust. (1957*a*)
Derwent Hunter	1956	C.S.I.R.O. Aust. (1957*b*)
Discovery II	Nov. 1930	Howard (1940)
Discovery II	June–July 1932	Discovery Committee (1941)
Discovery II	Oct. 1950–June 1951	Great Britain, National Institute of Oceanography (1957)
Ob	Apr. 1956	U.S.S.R. Academy of Sciences (1958)
Orsom III	Sept.–Oct. 1956	Rotschi (1957)
Planet	June 1908–July 1910	Reichard (1911)
Queenborough	Mar.–Apr. 1958	C.S.I.R.O. Aust. (1959)
Satsuma	July–Aug. 1956	Japan, Hydrographic Office (1958)
Shoyo-Maru	Aug.–Nov. 1956	Japan, Fisheries Agency (1957)
Umitaka-Maru	Jan. 1959	Tokyo University of Fisheries (unpublished data)

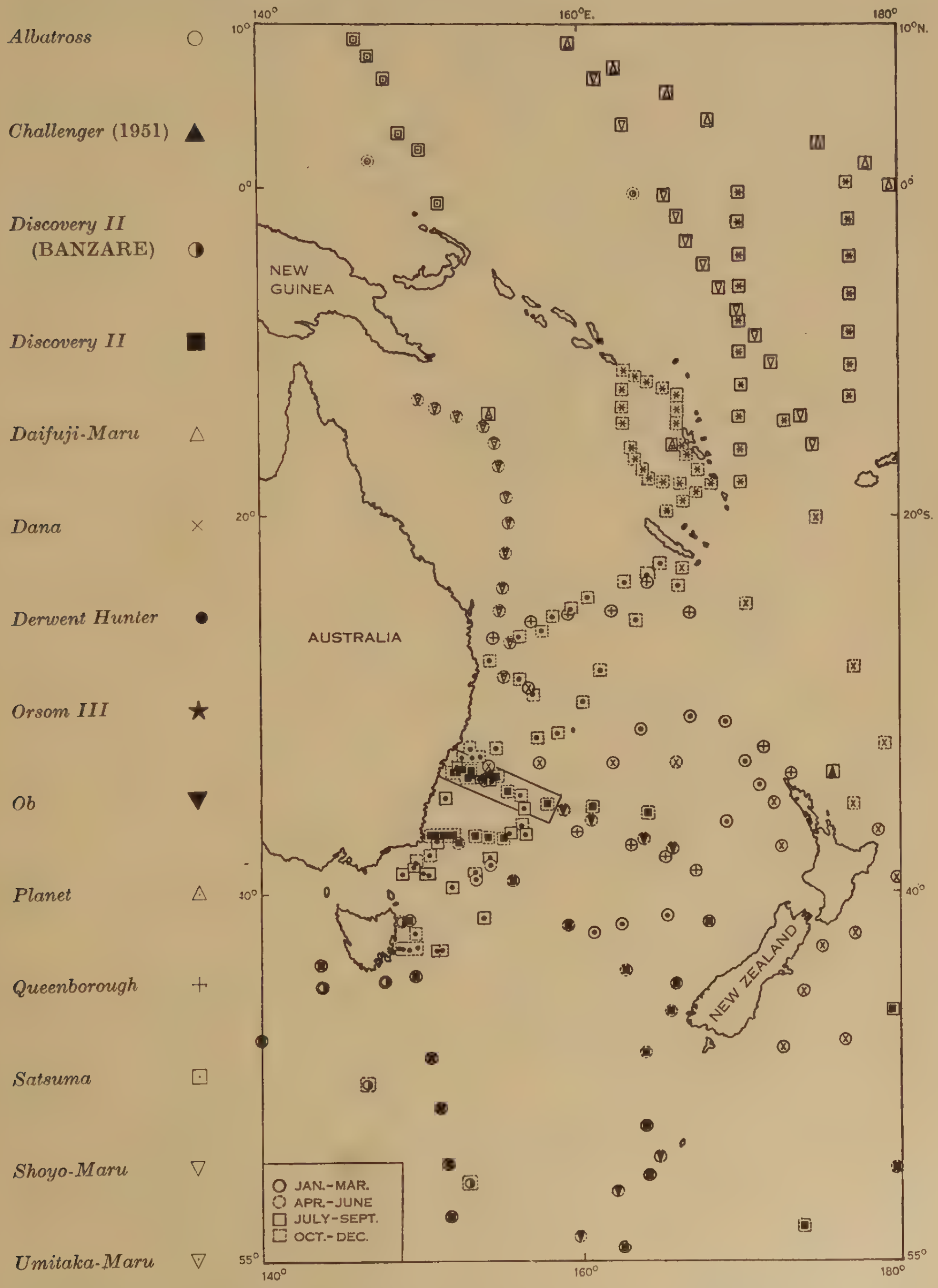
Table 2

ADDITIONAL SOURCES OF DATA USED IN SECTION IV

Vessel	Month and Year	Reference
Hugh M. Smith	June–Aug. 1950	Cromwell (1954)
Hugh M. Smith	Jan.–Mar. 1951	Austin (1954)
Hugh M. Smith	Jan.–Mar. 1952	Stroup (1954)
Hugh M. Smith	Aug.–Oct. 1956	Austin (1957)
Hugh M. Smith	Jan.–Mar. 1957	Wilson and Rinkel (1957)
Stranger	Aug.–Sept. 1956	Scripps Institution (1957)

(*b*) *Depth Distribution*

This surface deepened rapidly from the Antarctic Convergence to about 1000–1200 m at 45° S. and very gradually rose to depths of about 700 m at the equator (Fig. 3). As indicated in Section III(*a*) the core of the Antarctic Intermediate waters was probably 100 m deeper at the equator than the 27·20 σ_t surface.


Albatross ○
Challenger (1951) ▲
Discovery II (BANZARE) ◑
Discovery II ■
Daifuji-Maru △
Dana ×
Derwent Hunter ●
Orsom III ★
Ob ▼
Planet △
Queenborough +
Satsuma ⊡
Shoyo-Maru ▽
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NEW ZEALAND
JAN.-MAR.
APR.-JUNE
JULY-SEPT.
OCT.-DEC.

Fig. 1.—Map showing positions of stations used and quarters of the year in which stations were worked. Stations worked by *Derwent Hunter* on the repetitive section lines off Sydney (outlined area) in 1957–58 are not included.

Consideration of the direction of flow from depth contours (Montgomery 1938) is deferred to Section IV(a) so that it may follow the discussion of water type differentiation on this σ_t surface.

(c) *Salinity Distribution*

Maximum gradients in salinity were found to the east of Sydney and to the east of New Hebrides (Fig. 4). These were formed between the waters of highest salinity (34·60–34·70‰), extending south-west from the equator at about 180°, and northern extensions of South Pacific Ocean waters of low salinity (34·40‰), flowing into the Tasman Sea and into the region east of the New Hebrides.

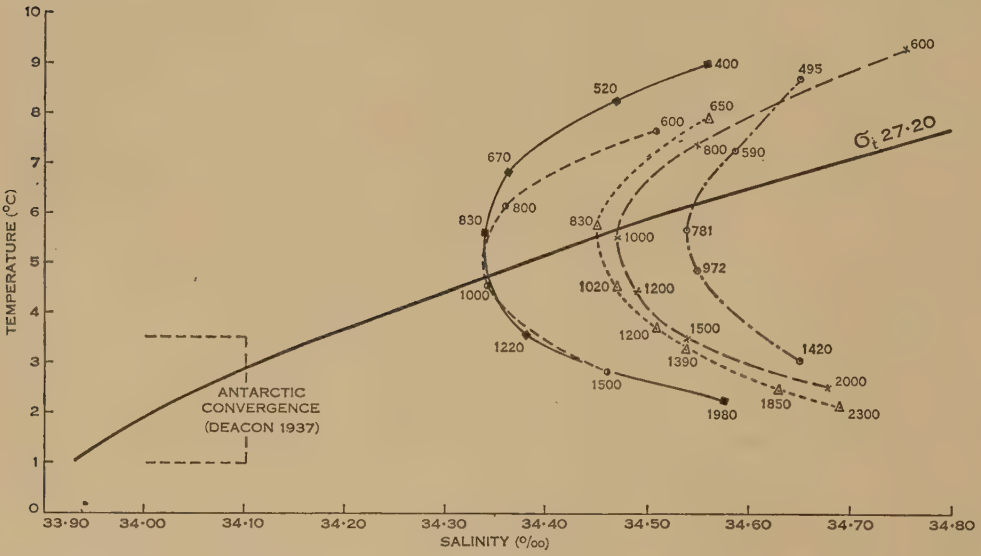


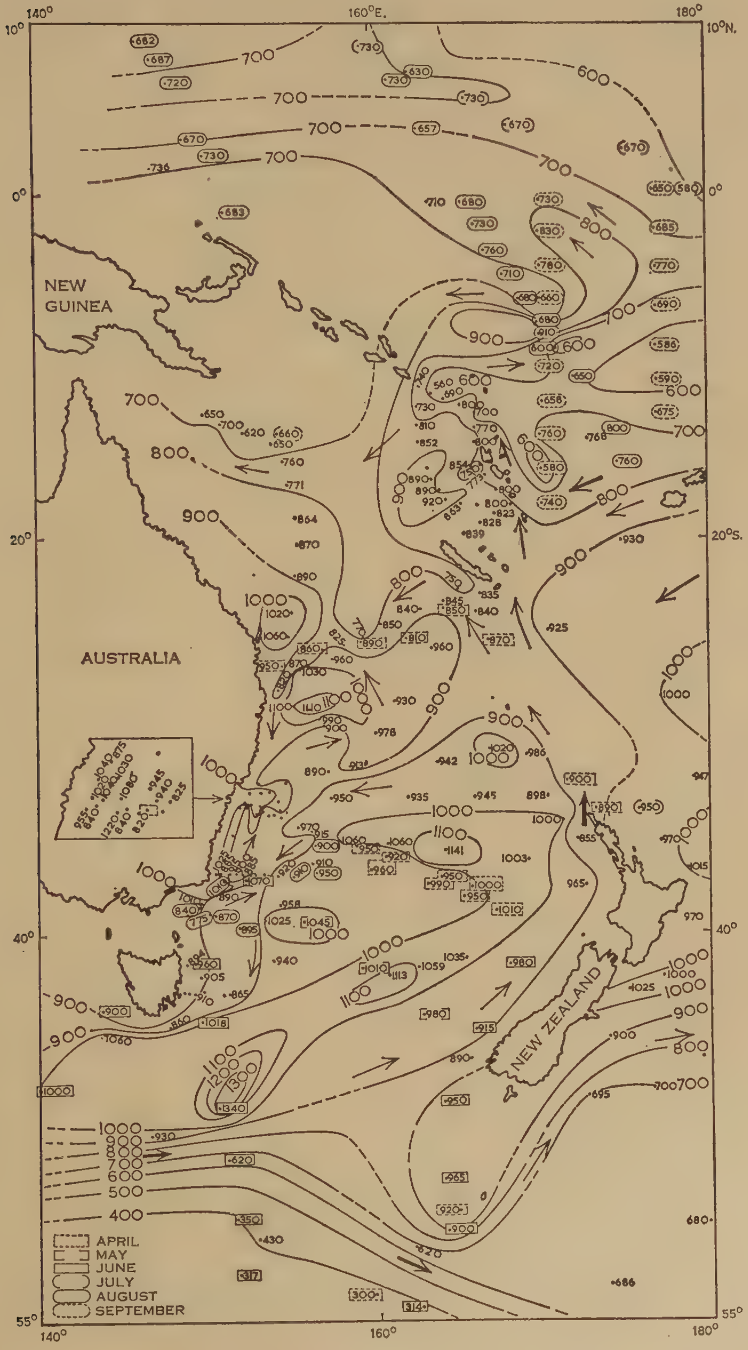
Fig. 2.—Salinity–temperature relations of selected stations.

Vessel	Station	Latitude	Symbol
Albatross	143	0° S.	⊙
Umitaka-Maru	13	20° S.	△
Dana	3366	30° S.	×
Discovery II	2727	35° S.	■
Discovery II	922	50° S.	◐

The limits of the temperature and salinity range of surface waters at the Antarctic Convergence are indicated.

(d) *Dissolved Oxygen Distribution*

The maximum oxygen gradients (Fig. 5) were formed in the regions of maximum salinity gradients (Fig. 4). In general the waters of low salinity had an oxygen content greater than 4·00 ml/l. and the waters of highest salinity of about 2·75 ml/l. The maximum oxygen values occurred in the extreme south-west of the region.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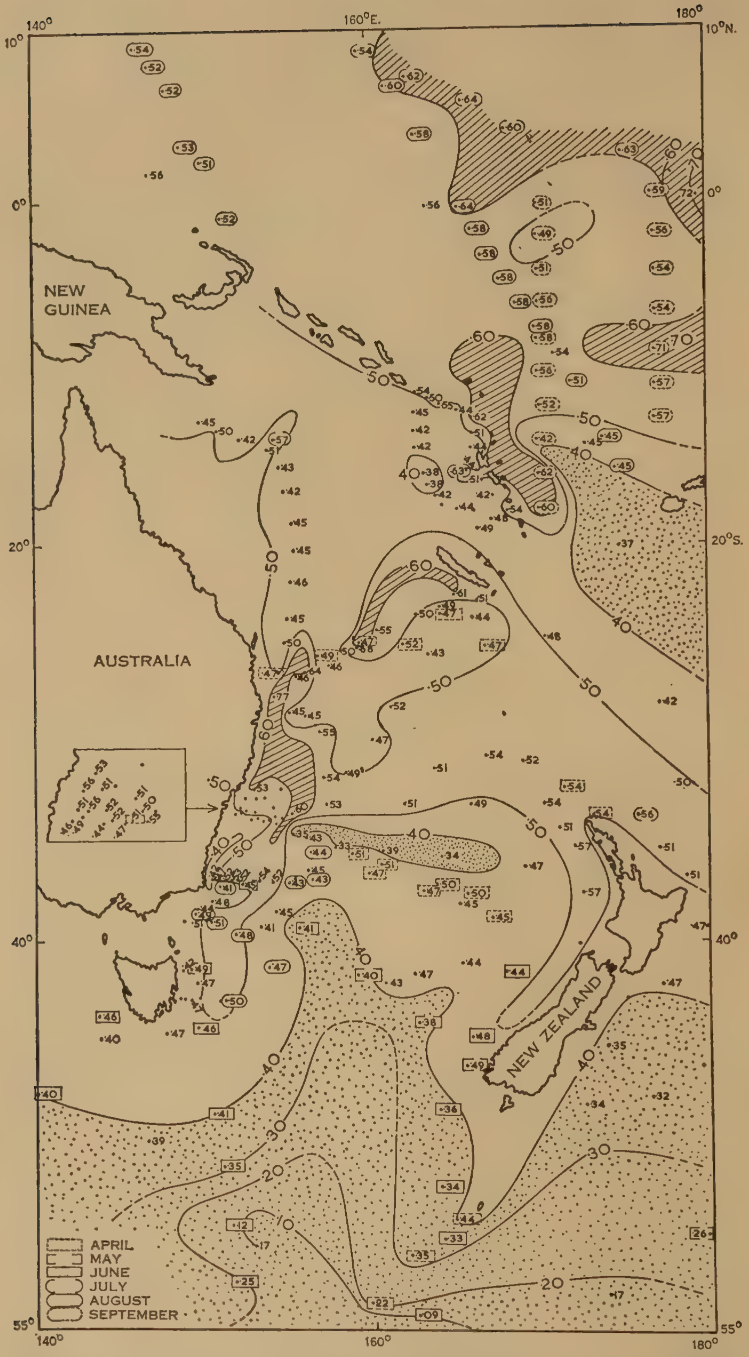
JUNE
JULY
AUGUST
SEPTEMBER

Fig. 3.—Depth of the 27·20 σ_t surface in the Tasman and Coral Seas (m). All data collected within the period of October to February are shown without brackets, the months of collection of other data are indicated by enclosed figures as listed. The arrows show the general circulation on this surface.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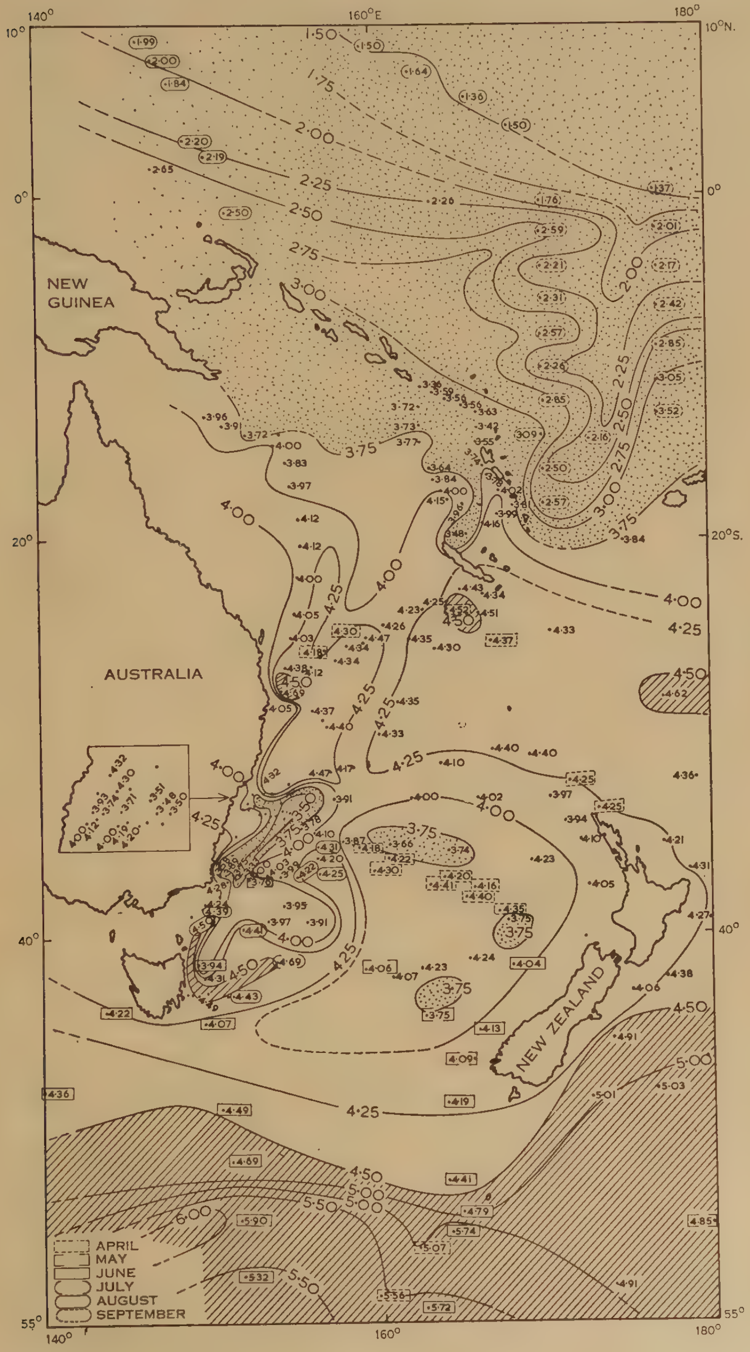
JULY
AUGUST
SEPTEMBER

Fig. 4.—Distribution of salinity on the 27·20 σ_t surface. Hatched areas indicate salinity greater than 34·60‰ and dotted areas salinity less than 34·40‰. All data collected within the period of October to February are shown without brackets, the months of collection of other data are indicated by enclosed figures as listed.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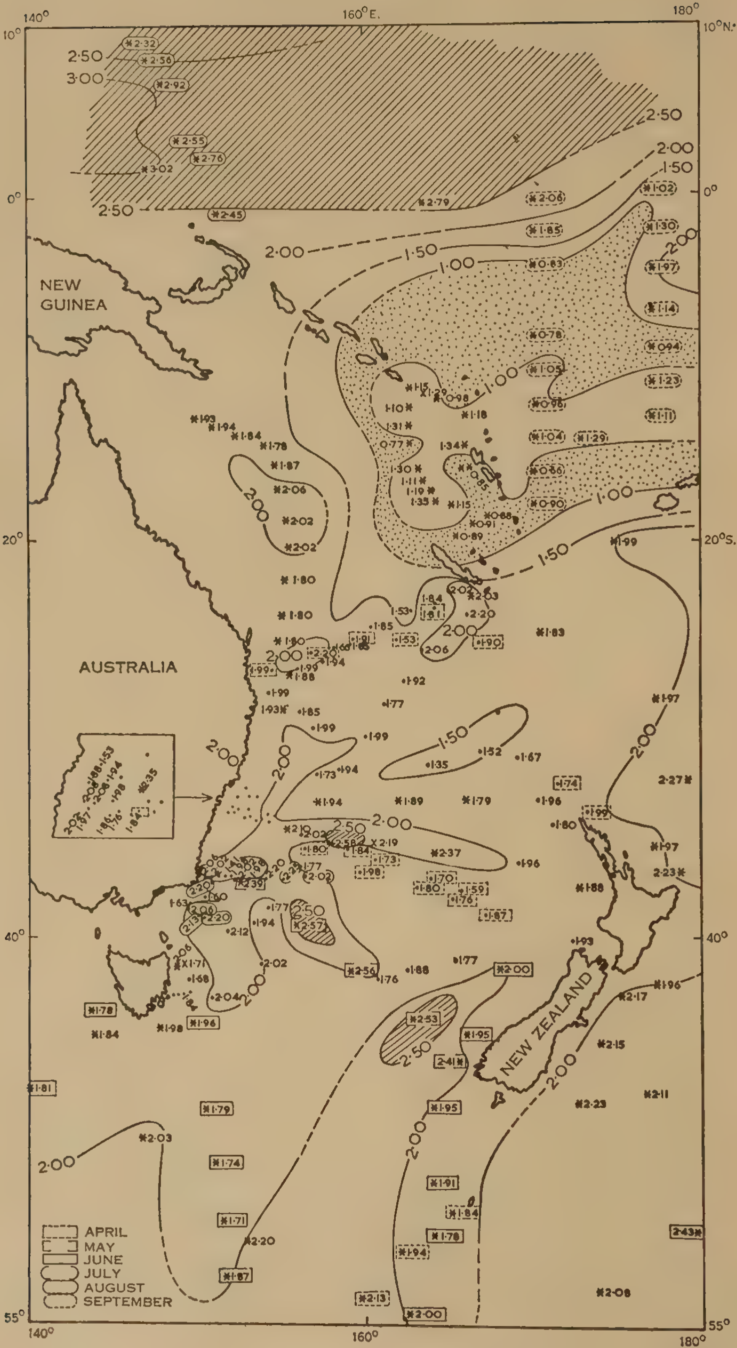
AUGUST
SEPTEMBER

Fig. 5.—Distribution of dissolved oxygen (ml/l.) on the 27·20 σ_t surface. Hatched areas indicate oxygen greater than 4·50 ml/l. and dotted areas oxygen less than 3·75 ml/l. All data collected within the period of October to February are shown without brackets, the months of collection of other data are indicated by enclosed figures as listed.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160°
180°
NEW GUINEA
AUSTRALIA
NEW ZEALAND
2·50
3·00
2·00
1·50
1·00
APRIL
MAY
JUNE
JULY
AUGUST
SEPTEMBER

Fig. 6.—Distribution of inorganic phosphates (●) and total phosphorus (★) on the 27·20 σ_t surface. Hatched areas indicate phosphate P greater than 2·50 µg-atom/l., and dotted areas phosphate P less than 1·00 µg-atom/l. All data collected within the period of October to February are shown without brackets, the months of collection of other data are indicated by enclosed figures as listed.

(*e*) *Phosphate Distribution*

In the region under consideration the maximum phosphate P values (2·50–3·00 μg-atom/l.) were found north of the equator around longitude 150° E. (Fig. 6). South of the equator tongues of water of low phosphate values (less than 1·00 μg-atom/l.), extended from the eastern boundary at about 10° S., and again at about 15° S., into the Coral Sea between New Caledonia and the Solomon Islands. These waters of low phosphate were in general associated with the waters of higher salinity (Fig. 4). The waters of low salinity (Section III(*c*)) had phosphate values of about 2·00 μg-atom/l.

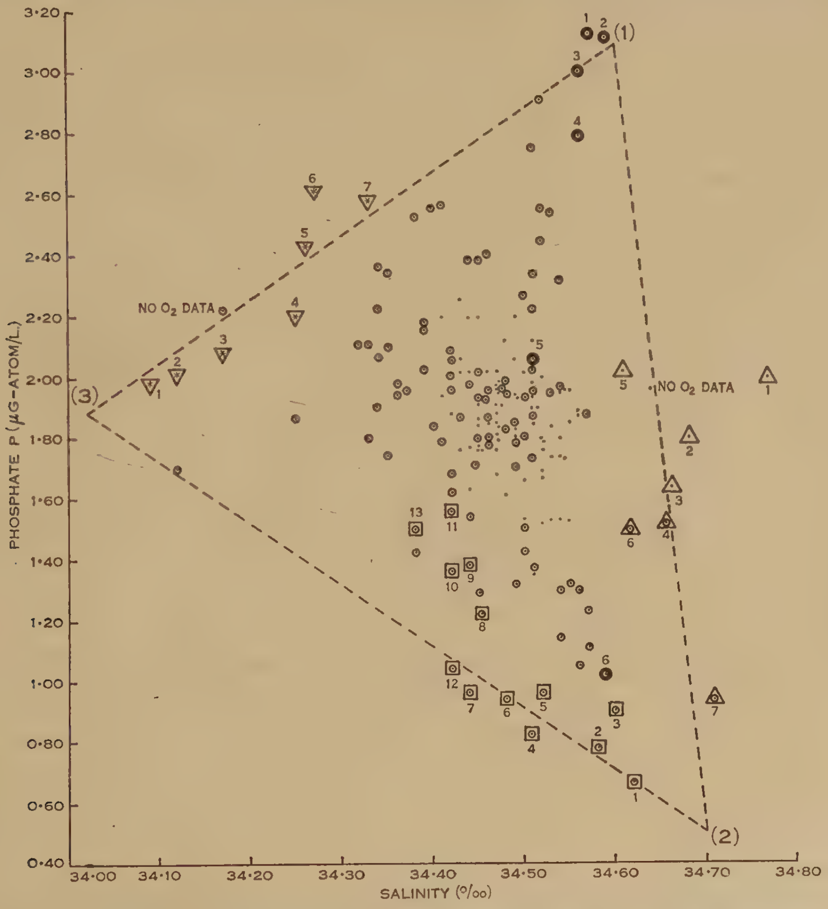


Fig. 7.—Salinity–phosphate relations on the 27·20 σ_t surface. Inorganic phosphate values, ⊙; total phosphorus values, ●. The numbered and coded values are used to locate boundary lines. The large figures 1–3 identify the three water types (Table 4).

IV. Discussion

(*a*) *Water Types on 27·20 σ_t Surface*

On this surface the phosphate to salinity relations varied considerably (Fig. 7). Boundary lines through the data indicate that at least three water types are needed to explain solely by mixing the observed salinity–phosphate combinations on the $27 \cdot 20\ \sigma_t$ surface. These waters are (1) salinity 34·60‰, phosphate P 3·10 μg-atom/l.; (2) salinity 34·70‰, phosphate P 0·50 μg-atom/l.; and (3) salinity 34·02‰, phosphate P 1·88 μg-atom/l.

The oxygen–salinity relations on this surface also varied considerably (Fig. 8) and these variations could be interpreted as mixtures of three water types with

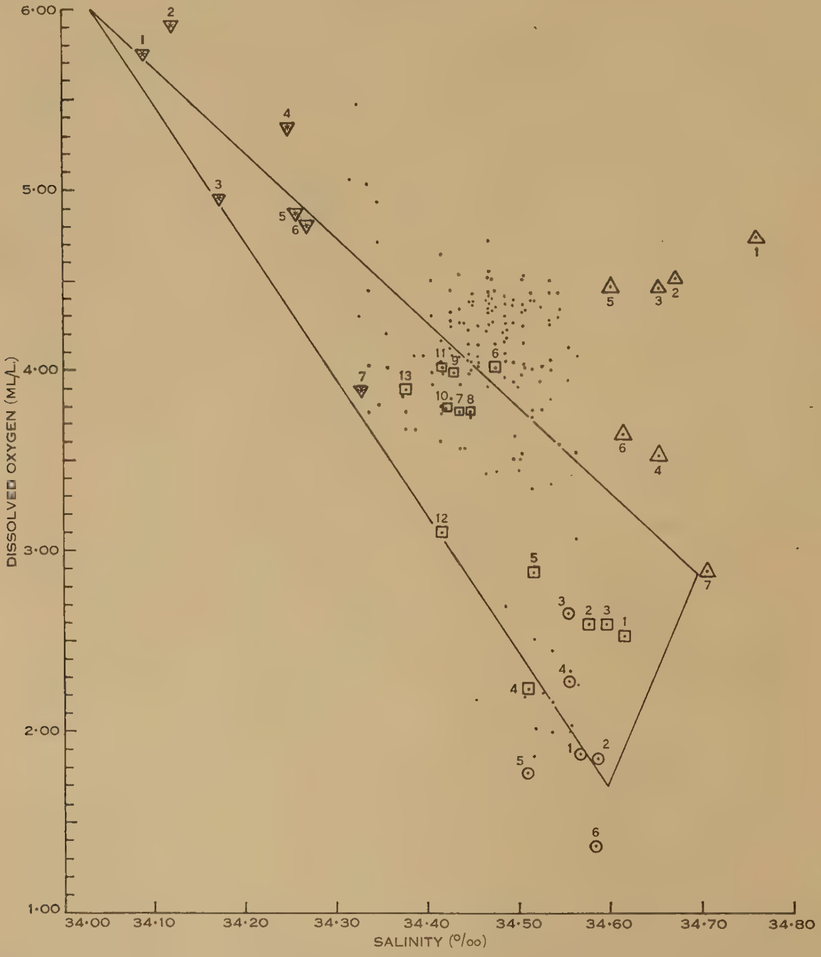


Fig. 8.—Salinity–oxygen relations on the $27 \cdot 20\ \sigma_t$ surface. The numbered and coded values of Figure 7 have been similarly identified, and used to locate boundary lines.

the same salinity values (Fig. 7). There is, however, no consistent agreement between the salinity–phosphate and the salinity–oxygen ratios of these data. A triangle, corresponding to the boundary triangle of Figure 7, has been fitted to the salinity oxygen diagram (Fig. 8) by using triangle value 7 and square values 1–3 which lie nearest to the position of water type (2), and circle values 1–4 which lie nearest to the position of water type (1) in Figure 7. At least half of the data in Figure 8 could not be explained as resulting from mixing of the three water types of Figure 7. Sverdrup, Johnson, and Fleming (1942) considered that discrepancies in the nutrient to oxygen depletion ratio of deeper waters were due to big latitudinal differences in the nutrient, but not oxygen, content of waters sinking from the surface. The same fact can cause the discrepancies between the phosphate and oxygen data of Figures 7 and 8. For these reasons it was considered more profitable to use phosphate rather than oxygen as a quasi-conservative identifying property for the water types on the 27·20 σ_t surface in the Tasman and Coral Seas.

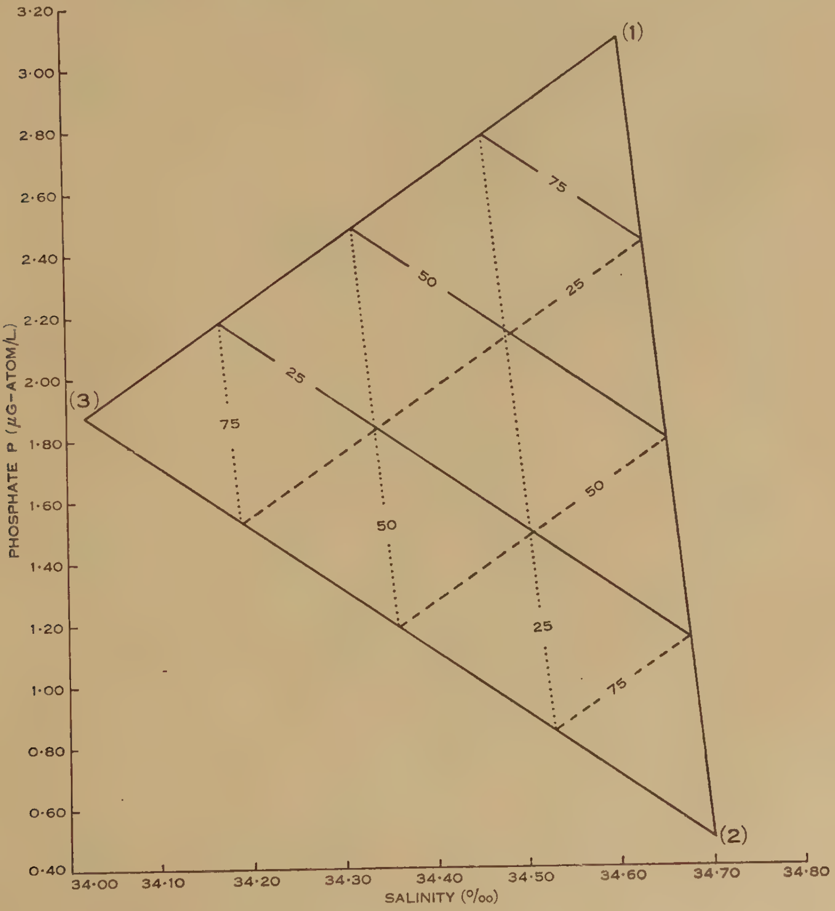
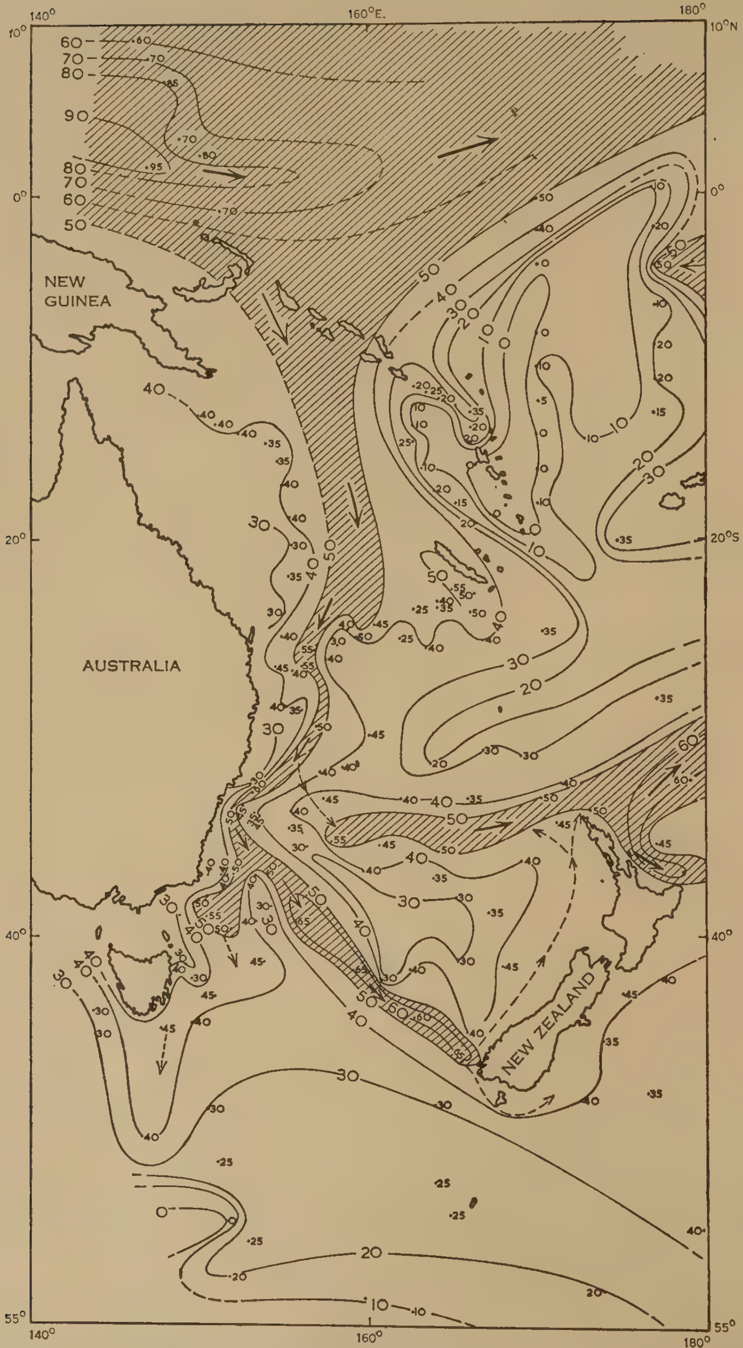


Fig. 9.—Salinity–phosphate mixing diagram for waters on the 27·20 σ_t surface.

(b) *Distribution of Water Types*

A mixing diagram (Fig. 9) prepared from the salinity–phosphate relations of Figure 7 was used to determine the percentage of each of the three water types on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NEW GUINEA
AUSTRALIA
NEW ZEALAND
60
70
80
90
80
70
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50
40
30
20
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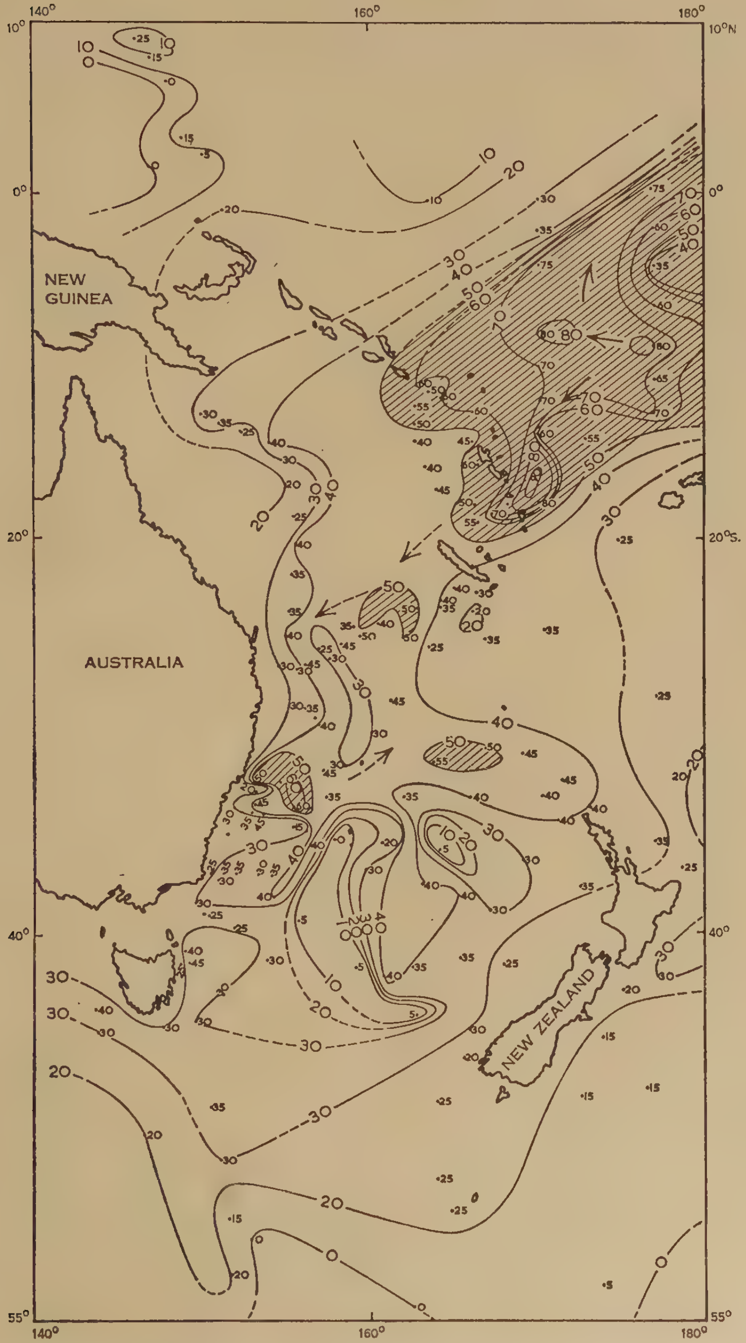
Fig. 10.—Percentage distribution of water type (1) (Table 4) on the σ_t surface. Hatched areas indicate where the percentage is greater than 50.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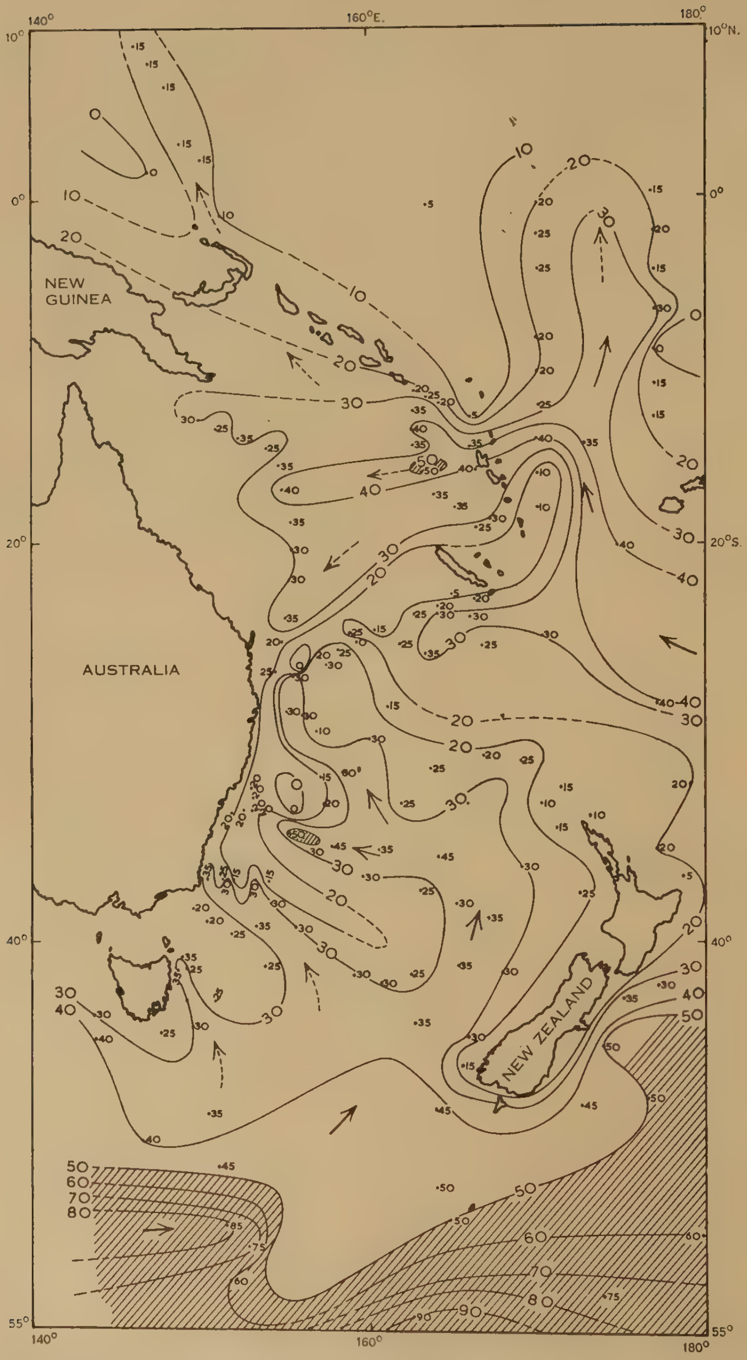
NEW ZEALAND

Fig. 11.—Percentage distribution of water type (2) (Table 4) on the 27·20 σ_t surface. Hatched areas indicate where the percentage is greater than 50.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90

Fig. 12.—Percentage distribution of water type (3) (Table 4) on the 27·20 σ_t surface. Hatched areas indicate where the percentage is greater than 50.

the 27·20 σ_t surface. In using this mixing diagram it was assumed that phosphates are nearly conservative on this surface and that mixing processes are almost entirely horizontal.

There is some evidence that vertical mixing of waters of the phosphate maximum (1500–2000 m) and the Antarctic Intermediate layer does occur in the Tasman Sea (Rochford 1960). As further data bearing on this point become available, some modification of the simplified approach to the interpretation of this section may be necessary.

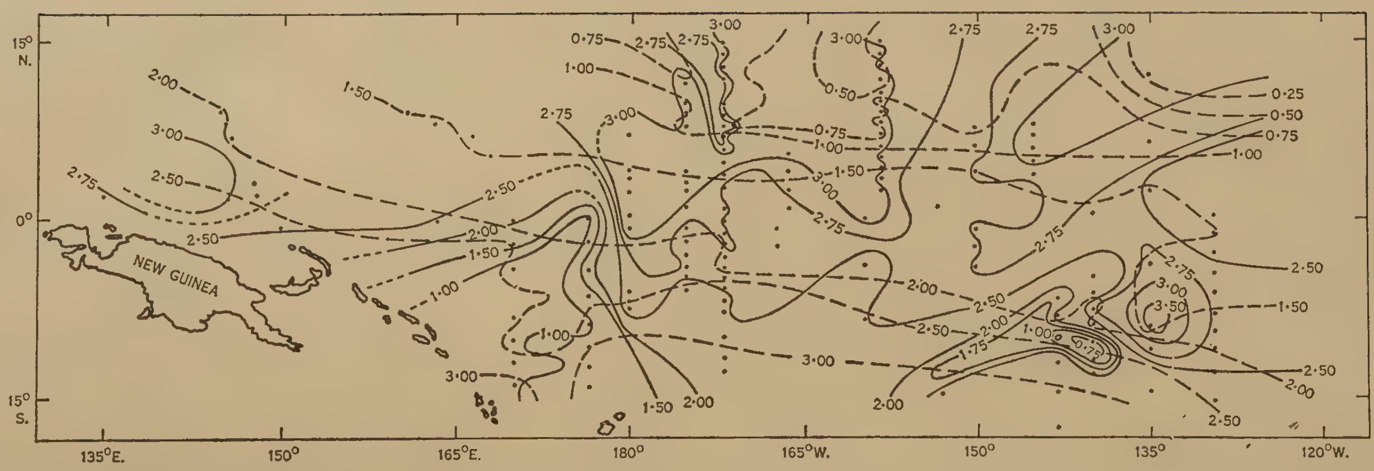
Water Type (1).—This water type was found in maximum concentration around the equator in the extreme north-west of the region (Fig. 10). To the south of the equator it was found in high concentration along the western margin from south of 20° S. to about 40° S. with two zonal extensions to the north and south of New Zealand. The distribution pattern indicates that there is continuity of this water type from the equator to about 40° S. although the number of stations in the central Coral Sea was insufficient to prove it. This drift path has been shown in Figure 10, but movement of water along the path is probably discontinuous and variable in amount. The drift path so derived (Fig. 10) and the general circulation based upon depth contours (Fig. 3) were in general agreement.

Water Type (2).—This water type was found in high concentration from the equator south-west to the New Hebrides, Solomon Islands, and New Caledonia (Fig. 11). Only three small regions of high concentration of this water type were found in the Tasman Sea south of New Caledonia. These were probably the surviving sections of a drift along the path indicated by the arrows in Figure 11. The depth contours of the 27·20 σ_t surface (Fig. 3) show a current to the west entering the region at about 15° S. This has a strong branch to the north around the New Hebrides and another to the south-west of New Caledonia. This latter current flows south along the western Tasman Sea to the region off Sydney (Fig. 3). These currents in general follow the distribution path of water type (2).

Water Type (3).—This water type occurred in maximum concentration in the extreme south of the region (Fig. 12), but it was found only in moderate concentration (30–50 per cent.) in the Tasman Sea, initially along the eastern margin, but then westward to east Australia in about latitude 35° S. A tongue of water of similar concentration also extended north-west into eastern Bass Strait. This water type also occurred at about the same concentration (40–50 per cent.) in the Coral Sea from the eastern margin around latitude 25° S. to the north and west of New Hebrides. Depth contours (Fig. 3) indicate a current flowing initially to the north and subsequently to the west along the distribution path of this water type. They also showed a westward flow, through the eastward margin, in about latitude 25° S., which could be continuous with the westward flow found in the Coral Sea in about latitude 15° S. These current paths are generally in agreement with the distribution of this water type.

(c) *Source Regions and Nomenclature of Water Masses*

The salinity phosphate properties of the three water types (Section IV(*a*)) have been deduced from Coral and Tasman Sea data. According to conventional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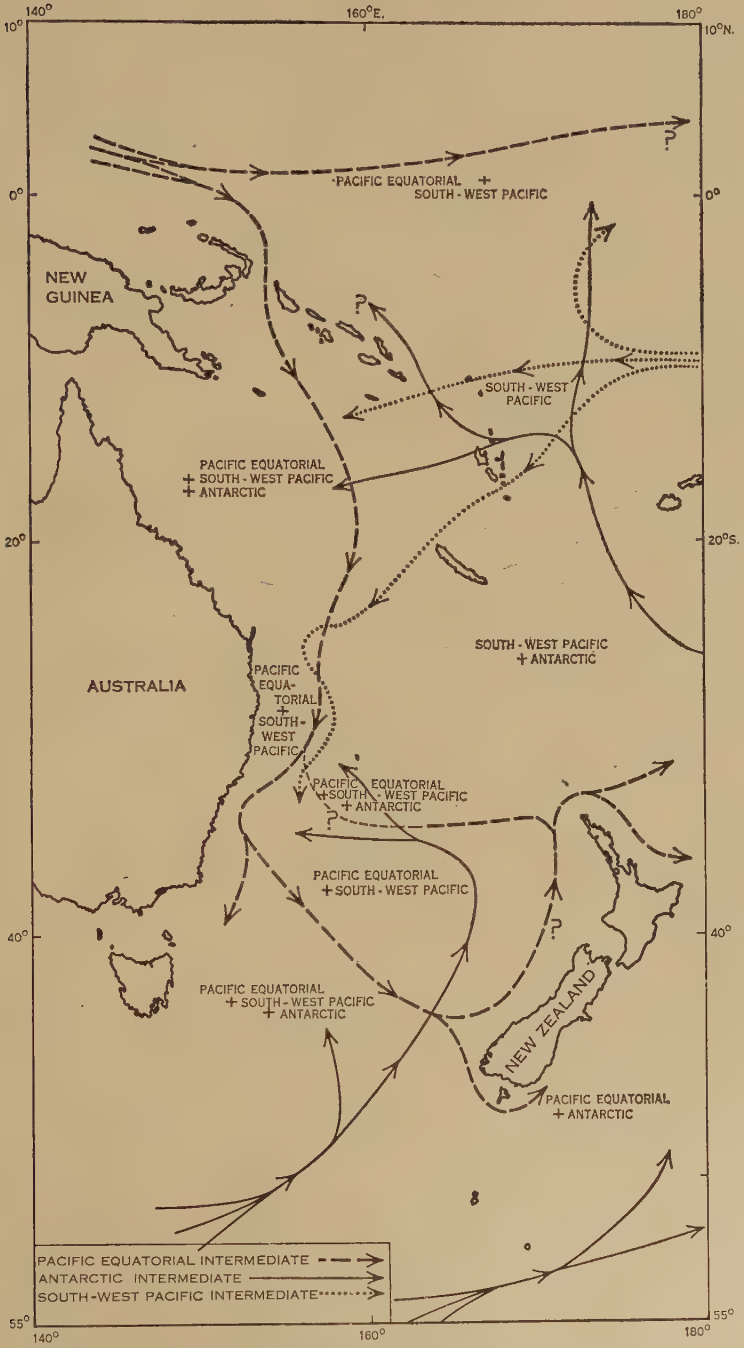
120°W.
NEW GUINEA
0·25
0·50
0·75
1·00
1·50
2·00
2·50
2·75
3·00
3·50

Fig. 13.—Distribution of phosphates (————) and dissolved oxygen (— — — —) in the region of the equator on the $27 \cdot 20\ \sigma_t$ surface in the Pacific, west of 120° W.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PACIFIC
PACIFIC EQUATORIAL
+ SOUTH - WEST PACIFIC
+ ANTARCTIC
20°
20°S.
SOUTH - WEST PACIFIC
+ ANTARCTIC
AUSTRALIA
PACIFIC
EQUA-
TORIAL
+
SOUTH-
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40°
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+ SOUTH - WEST PACIFIC
+ ANTARCTIC
NEW ZEALAND
PACIFIC EQUATORIAL
+ ANTARCTIC
?
PACIFIC EQUATORIAL INTERMEDIATE
ANTARCTIC INTERMEDIATE
SOUTH-WEST PACIFIC INTERMEDIATE
55°
55°
140°
160°
180°

Fig. 14.—General circulation of the three water types on the 27·20 σ_t surface of the Tasman and Coral Seas.

use the nomenclature of these water types is based upon their geographic sources which lie outside the Tasman and Coral Seas. Figure 13 shows the phosphate and oxygen distribution on the 27·20 σ_t surface along the equator in the Pacific Ocean to the west of 120° W. and between 15° N. and 15° S. (data from Table 2). It is not possible, from available data, to show the connection between the high phosphate waters to the north of New Guinea (water type (1), Fig. 8) and those to the east. However, at the same phosphate value (3·00 μg-atom/l.) waters to the east are much lower in oxygen. If these waters were originally at the surface, it follows that the high phosphate waters in the west are nearer their origin. This implies that these waters rich in phosphate are drifting to the east away from their origin. Their general circulation to the north of the Coral Sea would therefore be to the east (Fig. 14). These waters of very high phosphate content on the 27·20 σ_t surface are unique to the equatorial region, where high surface production (Steemann Nielsen 1953; Jitts and Rotschi 1957) accumulates phosphate-rich detritus in the waters down to the relatively shallow level of this layer (Fig. 3).

The waters along the 15° S. parallel are much lower in phosphate and higher in oxygen than those along the 15° N. parallel (Fig. 13). The decrease in phosphate values was especially pronounced around 140–150° W. and to the east of the New Hebrides (Fig. 6). The minimum phosphate values around 140–150° W. were found at Stations 45–46 of *Hugh M. Smith* Cruise 38, in 1957 (Table 2). The mean salinity of these waters was 34·58‰ which is less than that of the low-phosphate water type to the west (34·70‰, Fig. 8) but which was much higher than the salinity of the equatorial waters in the same region. The salinity value of the surface salinity maximum in the South Pacific probably exceeds 36·50‰ (Schott 1935) and minimum winter temperature of 14·5–15°C would be necessary for these waters to sink on to the 27·20 σ_t surface. Present knowledge of the distribution of these waters, with salinity high in relation to surface winter temperatures in the South Pacific, does not show the regions in which these combinations occur. However, there are indications (Rochford 1959) that waters of salinity 36·20‰ are found to the north of New Zealand where winter temperatures are within the critical minimum range. The surface waters of high salinity of the south-west Pacific have a low phosphate content (Rochford 1959). Probably, therefore, water type (2) with its low phosphate and relatively high salinity (Fig. 7) originates from the east of New Zealand between 35° and 40° S. and moves north on this surface (Fig. 13) into the two low-phosphate regions along the equator.

Waters with salinity and phosphate values similar to those of water type (3) were found by Deacon (1937) at the Antarctic Convergence (Table 3) to the south of the region discussed in this paper. Available data indicate that waters with such density, salinity, and phosphate values are unique to the Antarctic Ocean south of the Antarctic Convergence.

The probable geographic source of waters with properties similar to those of water types (1) and (3) has been shown. Their nomenclature (Table 4) is based upon their source regions. In the absence of hydrological data from the South Pacific Ocean the exact area where water type (2) is formed cannot be suggested. Without such a water type it is difficult to explain by advection the presence of waters of very low phosphate and high salinity values in the intermediate depths of the Tasman and Coral Seas, because horizontal mixing of water types (1) and (3) would produce phosphate levels at much higher values than were found in the Tasman and Coral Seas (Fig. 7). Mixtures of water types (1) and (3) would have to lose considerable amounts of phosphates, without change in salinity, to form the waters of type (2) with its very low phosphate values. Such losses could be caused by sedimentation of particulate phosphorus compounds if they formed about 50–60 per cent. of the total phosphorus (Fig. 7). Such a proportion of particulate phosphorus compounds is not to be expected at these depths (Ketchum, Corwin, and Kean 1955). Despite the uncertainty of its source, water type (2) has been tentatively called the South-West Pacific Intermediate of the Tasman and Coral Seas (Table 4).

TABLE 3

WATERS AT THE ANTARCTIC CONVERGENCE SOUTH OF AUSTRALIA

From Deacon (1937)

Discovery Section No.	Location	Temperature Range (°C)	Salinity Range (‰)	Mean Inorganic Phosphate P (μg-atom/l.)
10	Cape Leeuwin—south	4–5	33·90–34·00	—
11	Melbourne—south-west	3	33·90–34·00	1·72
12	Melbourne—south	3–4	33·90–34·00	1·52
13	New Zealand—south	3–4	33·90–34·10	1·69

TABLE 4

WATER TYPES ON THE 27·20 σ_t SURFACE IN THE TASMAN AND CORAL SEAS

Name	Salinity (‰)	Phosphate P (μg-atom/l.)
Antarctic Intermediate	34·02	1·88
Pacific Equatorial Intermediate	34·60	3·10
South-West Pacific Intermediate	34·70	0·50

(*d*) *General Circulation*

Figure 14, showing the general circulation on the 27·20 σ_t surface of the Tasman and Coral Seas, has been prepared from data on the distribution of the three water types (Figs. 10–12) and from the topography of this surface (Fig. 3). The lack of continuity towards the limits of their distribution of some of the water types (e.g. the isolated values of the South-West Pacific Intermediate greater than 50 per cent. in Fig. 11) was probably due to seasonal or year-by-year variation in the intensity of their movements. However, whatever the time scale involved, the circulation of the water types on this surface cannot be simultaneous, as Figure 14 might imply.

Because the Antarctic Intermediate water enters the Tasman and Coral Seas by separate paths (Fig. 14) its properties can be quite different in these two seas (Rochford 1960). The tongues of Pacific Equatorial Intermediate water across the Tasman Sea to the north and south of New Zealand are probably the escape routes for this water. The greater part of the Antarctic Intermediate water entering the Tasman Sea may escape by entrainment into one or other of these easterly movements.

In the Coral Sea the major escapement seems to be south into the western Tasman Sea, although there is an indication (Figs. 11 and 12) that mixtures of Antarctic and South-West Pacific Intermediate waters escape to the north of New Guinea, through the passage between New Britain and the Solomon Islands.

V. CONCLUSIONS

Salinity–phosphate relations indicate the presence of three water types on the $27 \cdot 20\ \sigma_t$ surface (Table 4).

(i) The Antarctic Intermediate water enters the Tasman and Coral Seas by separate paths, along their eastern margins. Its concentration is higher in the Coral than in the Tasman Sea.

(ii) The Pacific Equatorial Intermediate water enters the Coral Sea between New Britain and the Solomon Islands and is found in relatively high concentration as a continuous band along the western margin of the Tasman and Coral Seas, and eastwards to the north and south of New Zealand.

(iii) The South-West Pacific Intermediate water enters the region to the north of the Fiji Islands and spreads south-west to the New Hebrides. This water does not occur in high concentration in the Coral Sea, but occurs in isolated patches in the Tasman Sea.

VI. ACKNOWLEDGMENTS

The author is grateful to the Director of the National Institute of Oceanography for permission to use the library of the Institute, and to the Librarian for assistance in extracting data used in this paper.

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THE INTERMEDIATE DEPTH WATERS OF THE TASMAN AND CORAL SEAS

II. THE 26·80 σ_t SURFACE

By D. J. Rochford*

[*Manuscript received February 19, 1960*]

Summary

The distribution of salinity, dissolved oxygen, and phosphates on the 26·80 σ_t surface of the Tasman and Coral Seas is examined. The distribution patterns of these properties and the relations of salinity and phosphate and salinity and oxygen values are explained by horizontal mixing of three water types. These originated, one to the north of the Antarctic Convergence, one in the south-west Tasman, possibly in the Australian Bight, and one at the equator in the western Pacific. The major sinking regions and the circulation paths of subtropical waters in the Tasman Sea are deduced from their summer and winter distribution and from the topography of the 26·80 σ_t surface.

I. Introduction

This paper is a continuation of that dealing with the waters on the 27·20 σ_t surface in the Tasman and Coral Seas (Rochford 1960*a*). It examines the characteristics and distribution paths of the waters sinking at the Subtropical Convergence of the southern Tasman Sea, and of the other types of water with which they mix on the 26·80 σ_t surface in the Tasman and Coral Seas at depths between 200 and 700 m.

II. Material and Methods

The sources of all data have been given previously (Rochford 1960*a*). Because of possible seasonal effects a selection of the data according to seasons has been made; the greater part of them was collected during October to February, which corresponds to the period of major southerly flow of subtropical waters (Rochford 1958; Wyrtki, personal communication). Data from this period have been given emphasis in the preparation of Figures 1–4, and any other data have been labelled with the month of collection.

Phosphate values have been corrected for salt error as before (Rochford 1960*a*).

III. 26·80 σ_t Surface

(*a*) *Selection of this Surface*

The Subtropical Convergence in the southern Tasman Sea is found in waters with an average temperature of 11°C and salinity of 35·00‰ (Deacon 1937). Such waters have a σ_t of 26·80 and a surface with this value has been chosen to study the isentropic flow (Montgomery 1938) into the Tasman and Coral Seas of waters sinking at this convergence.

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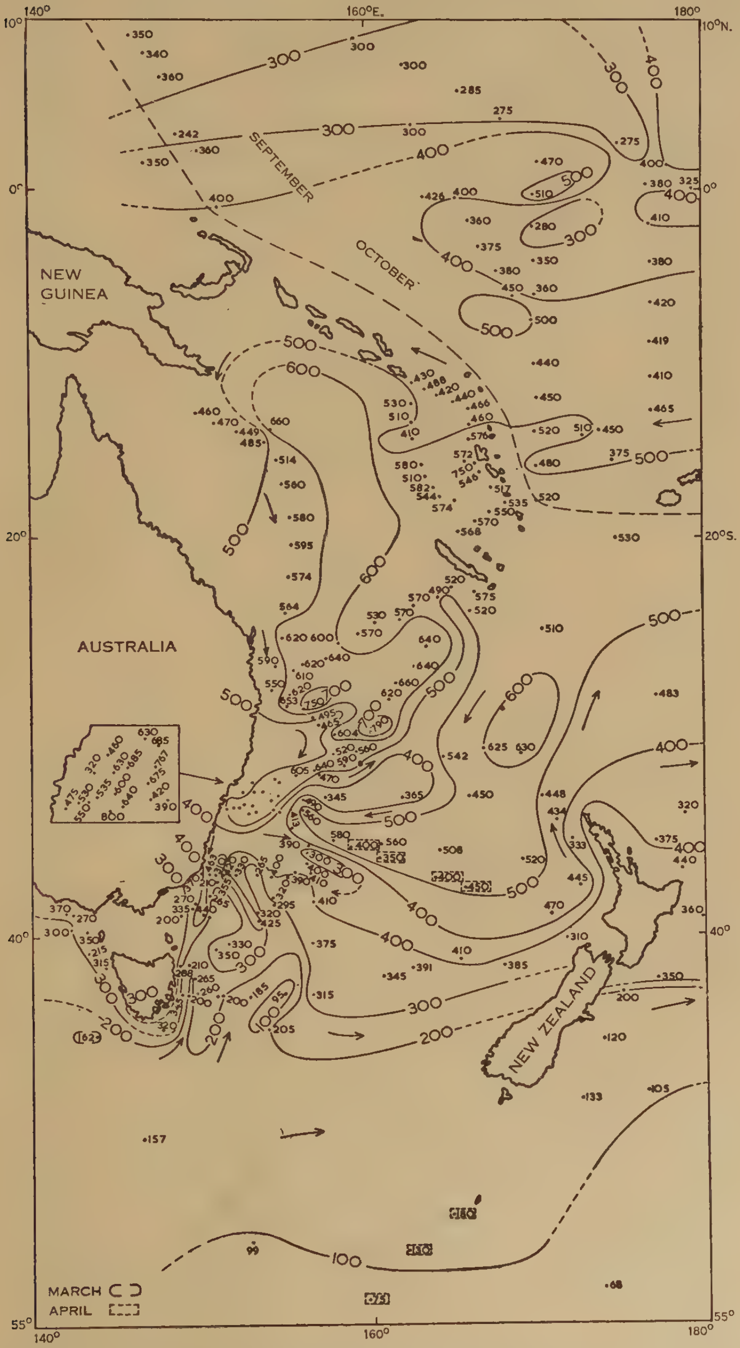
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NEW ZEALAND
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OCTOBER
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APRIL

Fig. 1.—Depth (m) of the 26·80 σ_t surface during October to February. Data from other months have been identified separately.

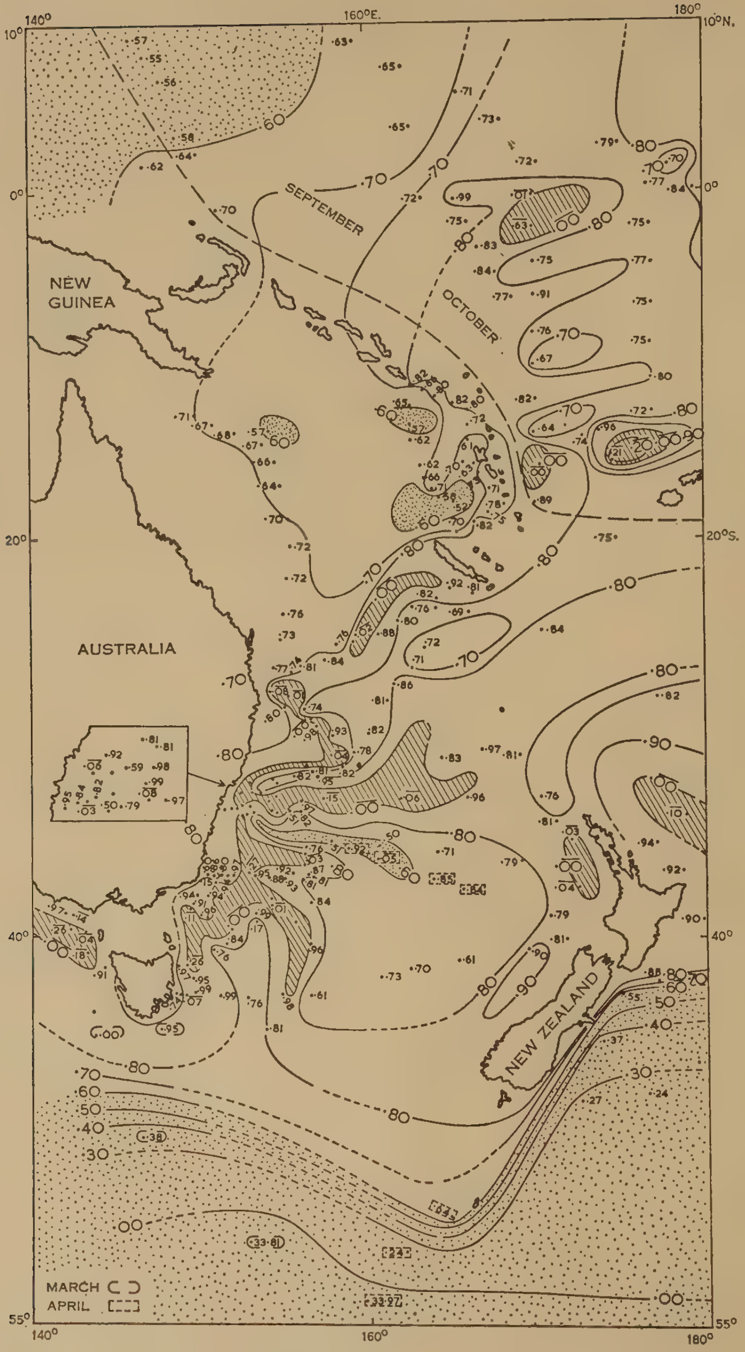
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Fig. 2.—Distribution of salinity on the 26·80 σ_t surface (values below 34·00‰ given in full, those between 34·00‰ and 34·99‰ shown by figures after decimal point, and those above 35·00‰ as barred figures). Hatched areas indicate salinity greater than 35·00‰ and dotted areas salinities less than 34·60‰.

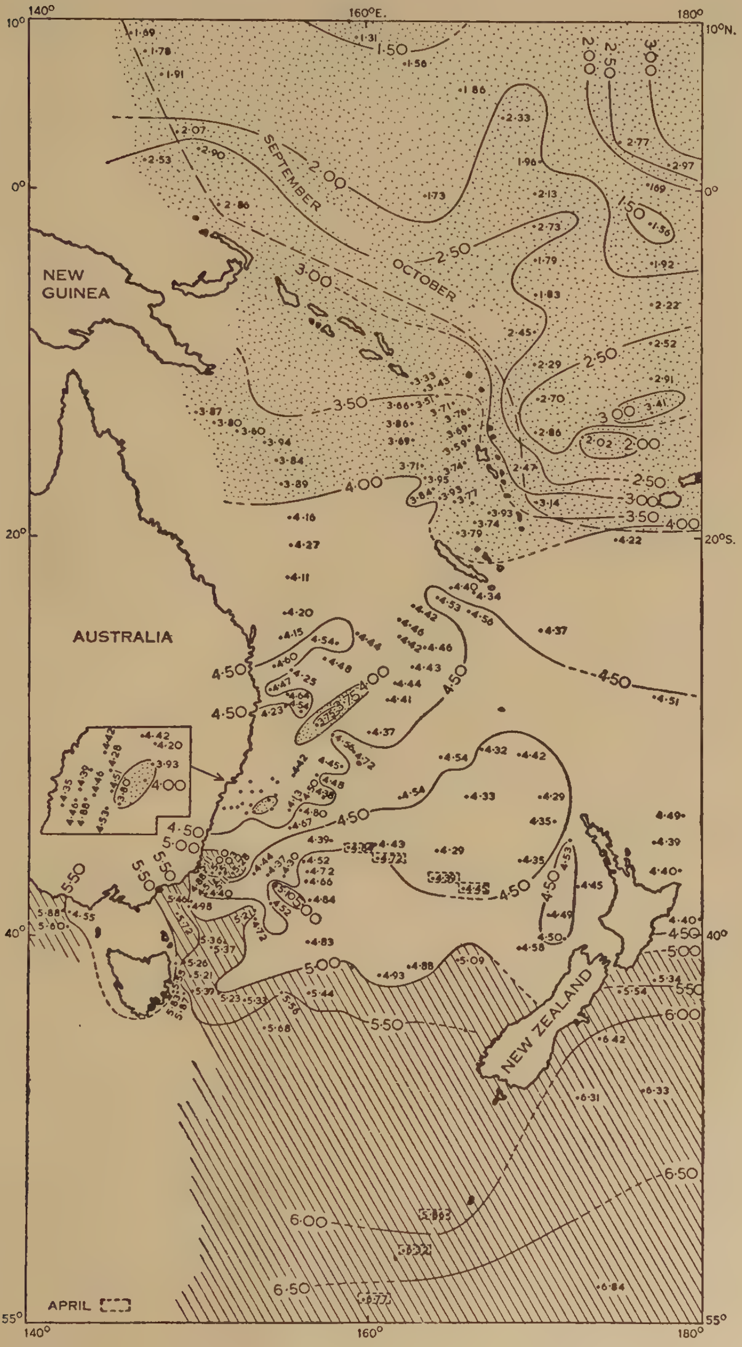
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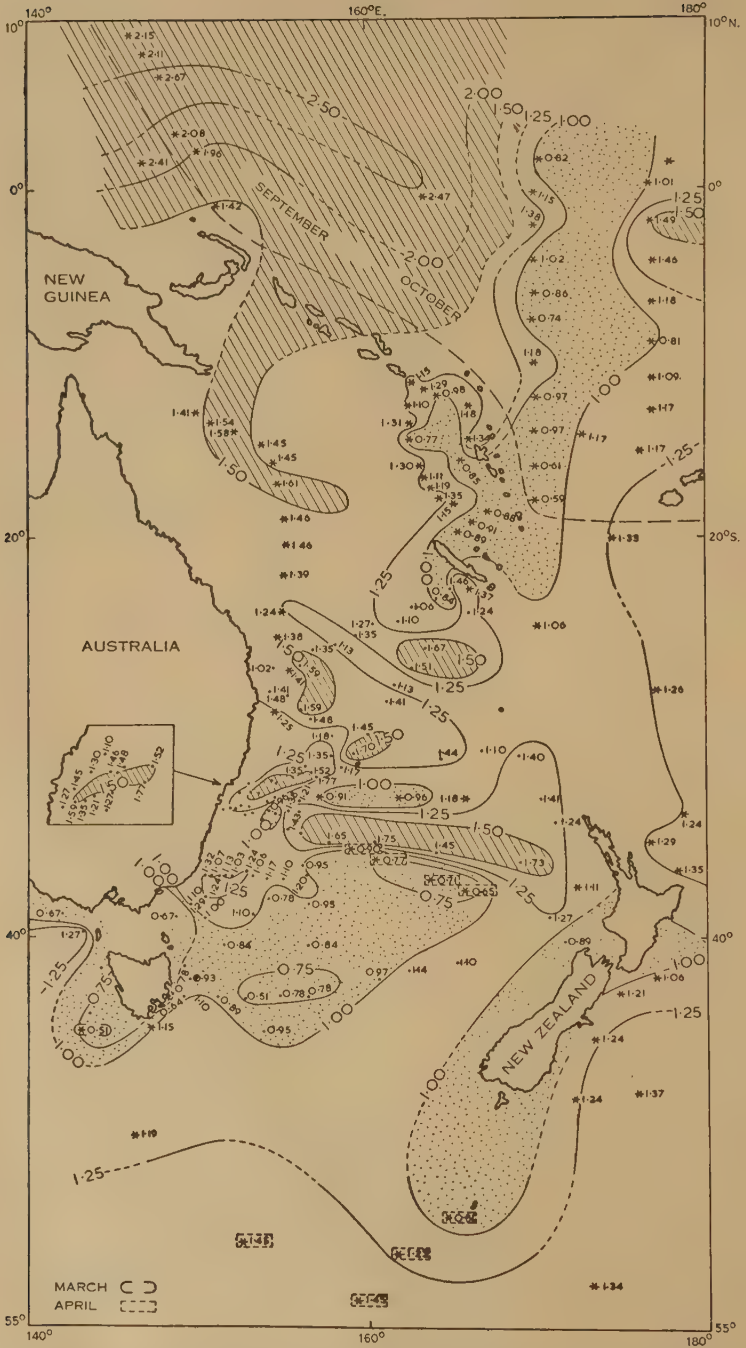
Fig. 3.—Distribution of dissolved oxygen (ml/l.) on the 26·80 σ_t surface. Hatched areas indicate oxygen content greater than 5·00 ml/l. and dotted areas indicate oxygen content less than 4·00 ml/l.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MARCH
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*1·58
*1·45
*1·61
*1·46
*1·39
*1·24
*1·38
*1·06
*1·26
*1·24
*1·29
*1·35
*1·41
*1·06
*1·21
*1·24
*1·37
*1·34
*1·19
0·67
1·27
0·93
0·51
0·84
0·78
0·95
0·97
1·14
1·40
1·10

Fig. 4.—Distribution of inorganic phosphates (*) and total phosphorus (●) on the 26·80 σ_t surface. Hatched areas indicate phosphate P content greater than 1·50 μg-atom/l., dotted areas phosphate P content less than 1·00 μg-atom/l.

(b) *Depth Distribution*

The 26·80 σ_t surface was found at maximum depths of about 600–700 m in the western Tasman and Coral Seas (Fig. 1). From this region this surface gradually shallowed along the western margin to about 100 m in the extreme south and 300 m in the north. Eastwards of Sydney it rose rather steeply to depths of 300–400 m and maintained this depth along the eastward margin.

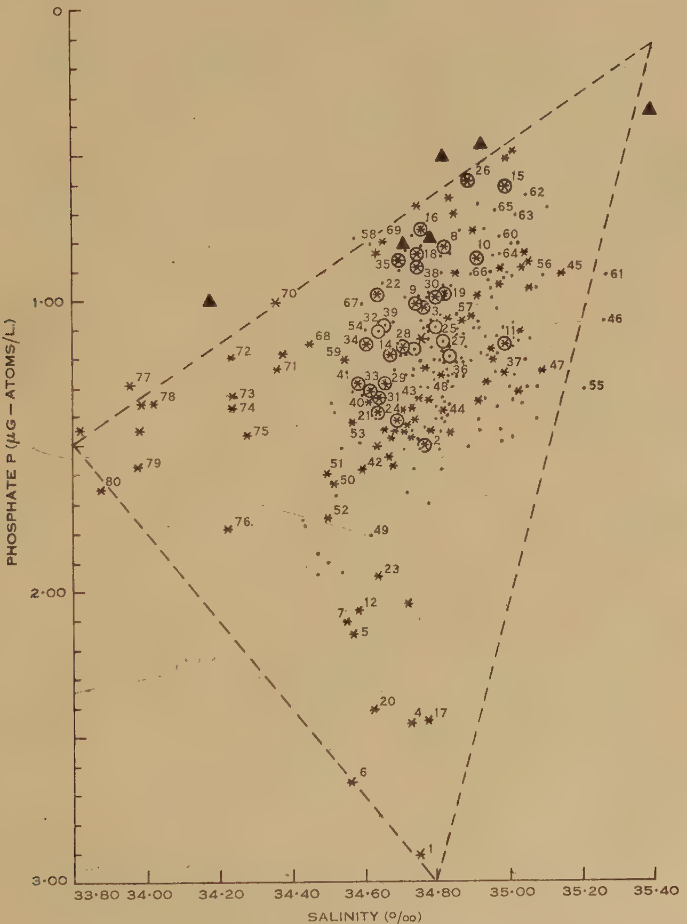


Fig. 5.—Salinity–phosphate relations of water on the 26·80 σ_t surface; inorganic phosphates,*; total phosphorus,●. Numbered values refer to waters whose salinity–oxygen characteristics have been similarly identified in Figure 6. ▲ indicates *Ob* data from the Australian Bight. Circles indicate values for oxygen and phosphates, which do not correspond.

(c) *Salinity Distribution*

On this surface salinities ranged from 34·00‰ in the extreme south to 35·00–35·20‰ in the north-east (Fig. 2). These waters of high salinity extended south-west from the equator around 170° E. to northern Tasmania and western Bass Strait. They were also found to the north-west and north-east of New Zealand.

(*d*) *Dissolved Oxygen Distribution*

In the Tasman Sea, waters with dissolved oxygen values higher than 5·00 ml/l. were confined to the region south of 40° S., except off the south-east Australian coast, where a northern extension occurred (Fig. 3). North of 20° S. the oxygen values decreased towards the equator, but more rapidly on the eastern side of the region, especially between Fiji and the New Hebrides.

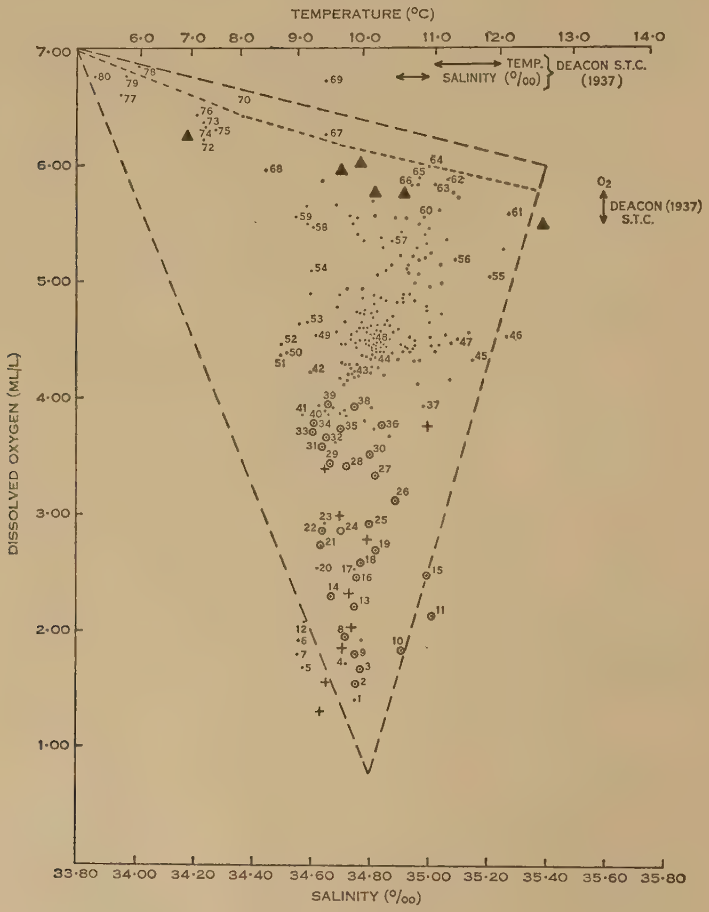


Fig. 6.—Salinity–oxygen relations of waters on the 26·80 σ_t surface. See Figure 5 for significance of numbered, circled, and triangle values. The temperatures required for a σ_t value of 26·80 at different salinities and the range of salinity–temperature and oxygen values at the subtropical convergence are given. + indicates no phosphate values to correspond with those in Figure 5. The line of smaller dashes indicates oxygen saturation of waters with different salinities on the 26·80 σ_t surface.

(*e*) *Phosphate Distribution*

Phosphate P concentrations of less than 1·00 μg-atom/l. were found in the southern Tasman Sea to the west of 160° E. (Fig. 4). Around Tasmania and New

Zealand these waters extended further south in the autumn (Fig. 4, April values). A belt of these waters was found during August to September between New Caledonia and the equator. Waters of higher phosphate P concentrations (1·5 μg-atom/l. or more) were mainly confined to the northern Coral Sea and the equator west of about 170° E. Isolated occurrences of such waters were found in the Tasman Sea south to about latitude 35° S.

IV. Discussion

(a) *Water Types on the 26·80 σ_t Surface*

On this surface phosphate values varied independently of salinity, especially at higher salinities (Fig. 5), and this is true also of oxygen values (Fig. 6). Mean boundary lines on Figure 5 show that a minimum of three water types (Table 1) would be needed to explain solely by mixing the observed phosphate–salinity relations (Fig. 5). Salinities of the three water types (Table 1) were used to position boundary lines around the salinity–oxygen data (Fig. 6). The circled values in this figure do not correspond to the relative position of their counterparts in Figure 5, and were probably caused by secondary oxygen utilization independently of phosphate release. These values were from the New Hebrides area where similar oxygen anomalies were found on the 27·20 σ_t surface (Rochford 1960*a*). In general, however, water type (1) (Figs. 5 and 6, values 1, 4, 5, 6, 7, 12) has an oxygen content of less than 2·00 ml/l.; water type (2) (Figs. 5 and 6, values 55, 56, 61, 65) has between 5·00 and 6·00 ml/l., and type (3) (Figs. 5 and 6, values 77–80) has between 6·00 and 7·00 ml/l. (Table 1).

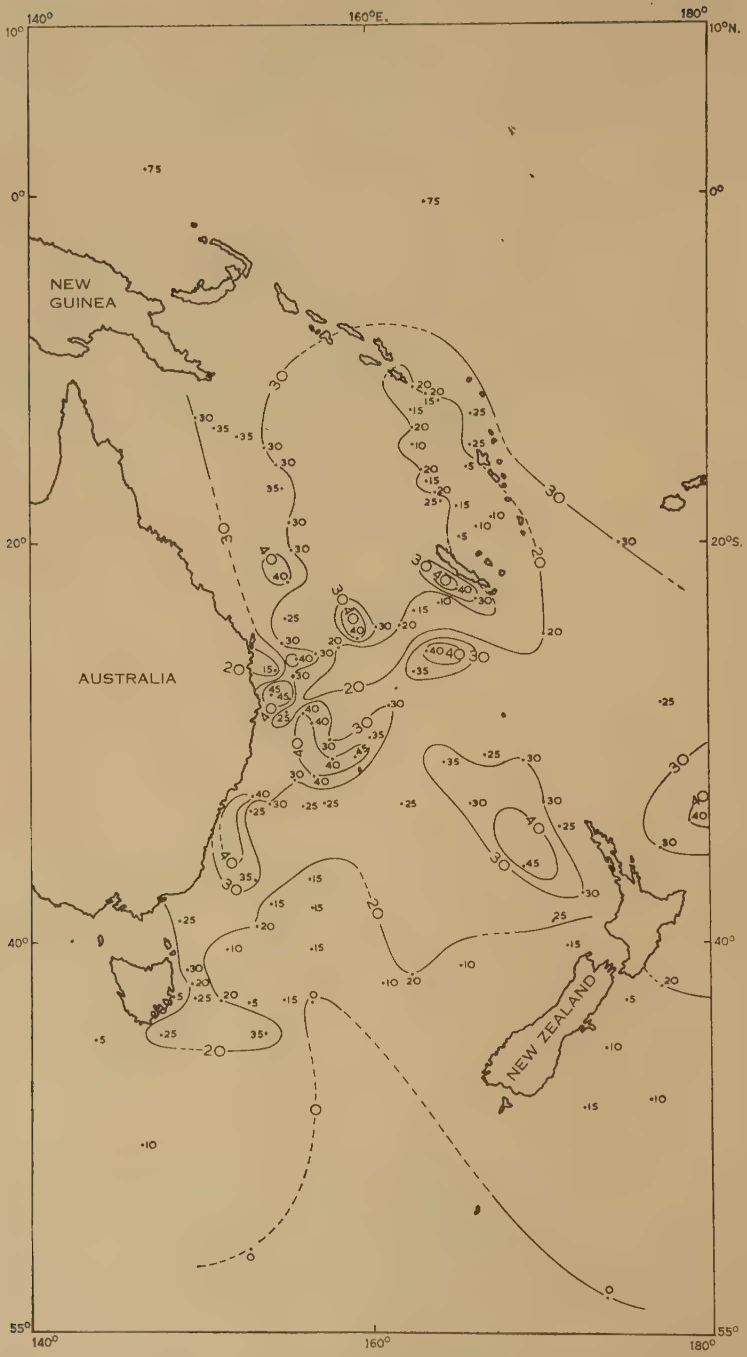
Table 1

WATER TYPES ON THE 26·80 σ_t SURFACE OF THE TASMAN AND CORAL SEAS

Water Type	Name	Salinity (‰)	Oxygen (ml/l.)	Phosphate P (μg-atom/l.)
(1)	Upper Equatorial Intermediate	34·80	<2·00	2·50–3·00
(2)	Subtropical	35·20–35·40	5·00–6·00	<0·50
(3)	Upper Antarctic Intermediate	33·80–34·00	6·00–7·00	1·40–1·60

(b) *Distribution of Water Types*

Only during the summer period, November to February, were sufficient data available to prepare charts of the distribution of water types within a particular season. During the winter, when sinking at convergences would be facilitated by maximum surface densities, data were limited to the southern Tasman Sea and the extreme north-east of the region. It is proposed, therefore, to consider the summer distribution throughout the region and the winter distribution for the southern Tasman Sea only. A mixing triangle (Rochford 1960*a*) was used to calculate the percentage amounts of each of the water types (Table 1).



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40°
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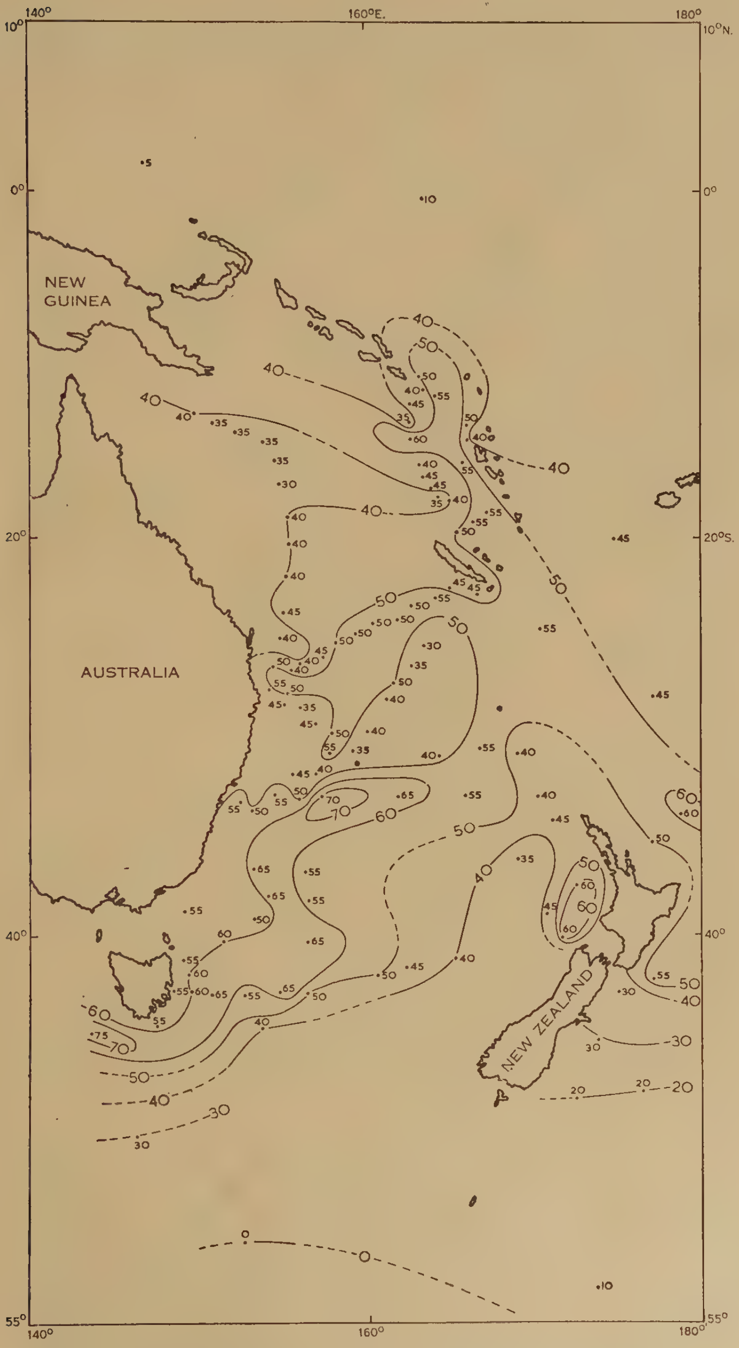
55°
140°
160°
180°
NEW GUINEA
AUSTRALIA
NEW ZEALAND

Fig. 7.—Summer (November-February) distribution of the percentage of water type (1) on the 26·80 σ_t surface.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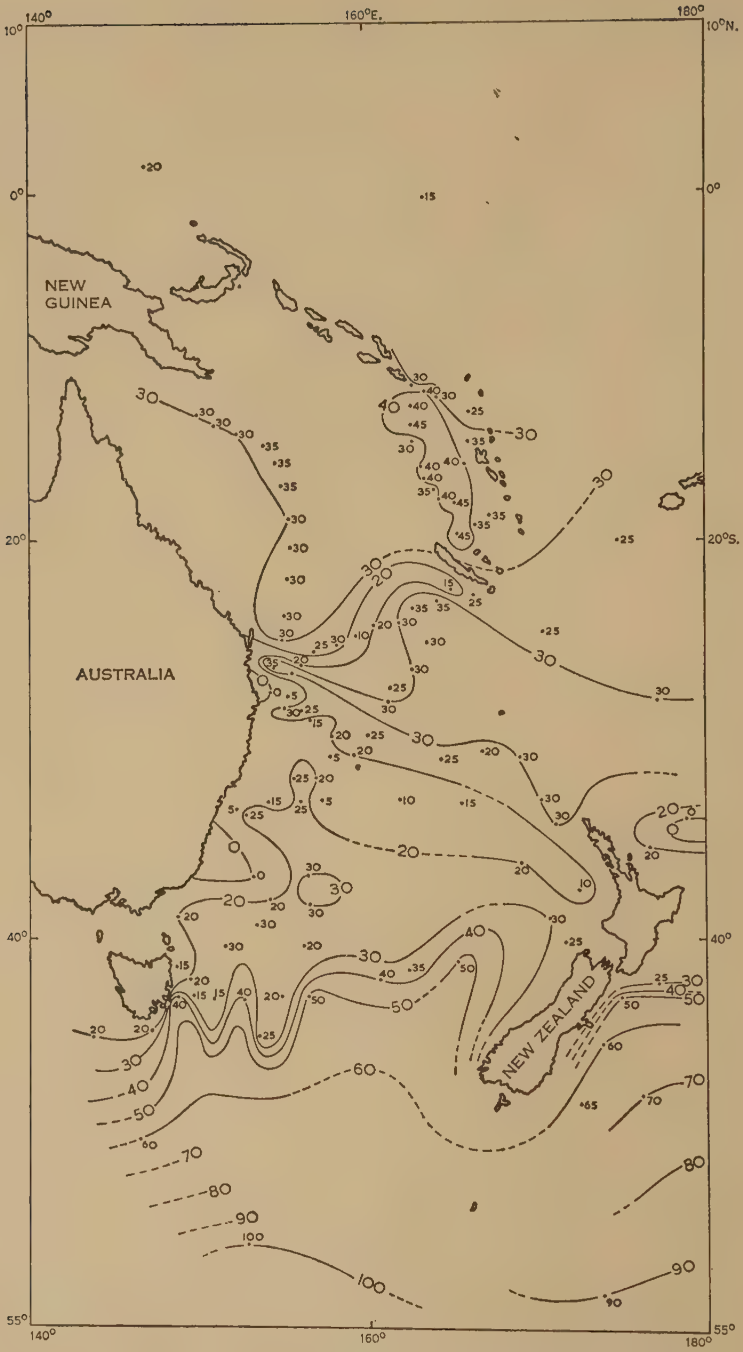
NEW GUINEA
AUSTRALIA
NEW ZEALAND
40
50
60
70
30
20
0

Fig. 8.—Summer distribution of the percentage of water type (2).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NEW GUINEA
AUSTRALIA
NEW ZEALAND
30
40
20
50
60
70
80
90
100

Fig. 9.—Summer distribution of the percentage of water type (3).

(i) *November to February*

Water Type (1).—This water type was not extensively distributed nor found in high concentration in the region (Fig. 7). Maximum values of 40–45 per cent. were confined to the region 20–40° S., and their distribution suggests that the major flow paths of this water type were linked with the upper and possibly also with the deeper circulation of equatorial waters (Rochford 1958, 1960*b*). Southward movements on the 26·80 σ_t surface along the western margin of the Coral and northern Tasman Seas, as shown by the topography (Fig. 1), and some of the zonal circulation to the east between 30–40° S. (Fig. 1), were probably part of the circulation pattern of this water type.

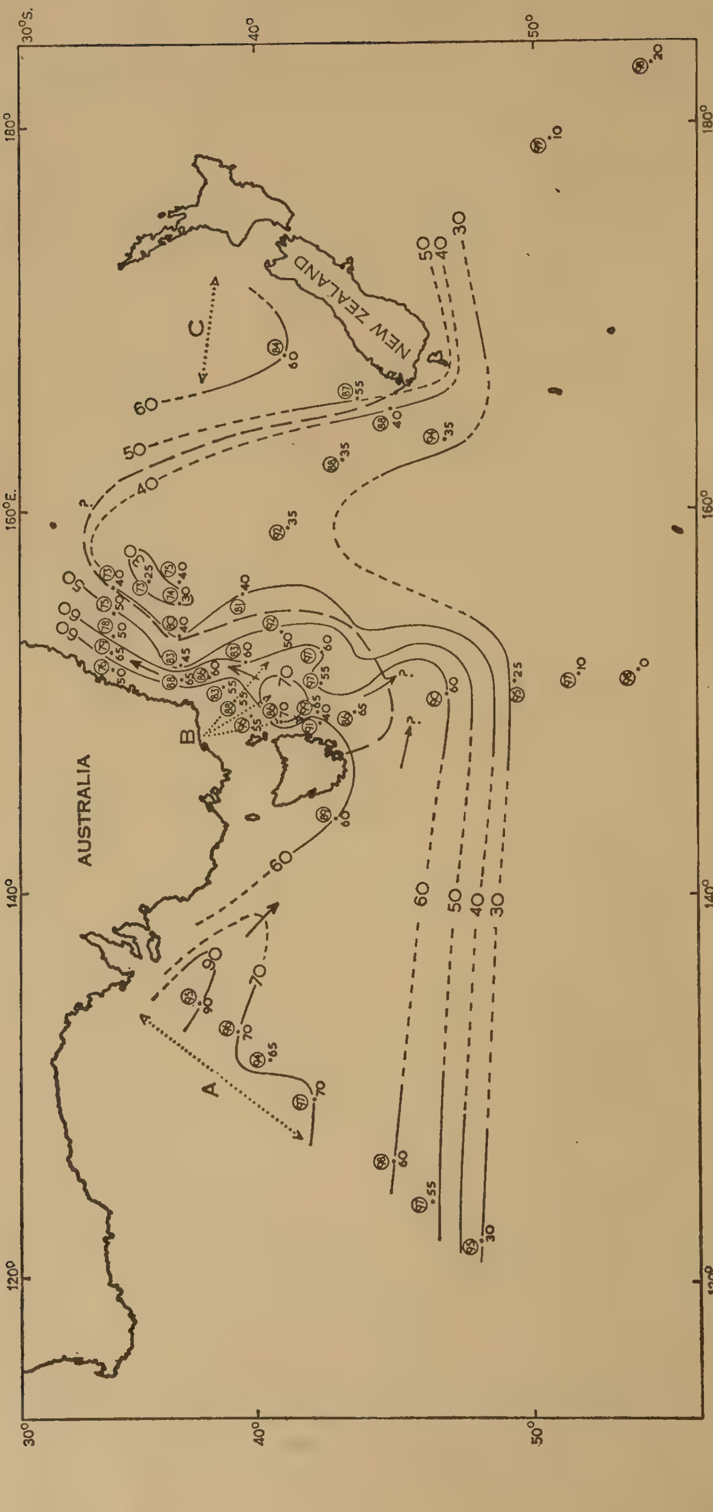
Water Type (2).—This water type was found at concentrations greater than 50 per cent. from the extreme south-west Tasman Sea through to New Zealand, New Caledonia, and the Solomon Islands (Fig. 8). It was the dominant water type on the 26·80 σ_t surface. Maximum concentrations of this water type were found in the south-west Tasman Sea. Movements from there in a general north-easterly direction could account for its distribution elsewhere. The topography of the 26·80 σ_t surface, however, shows that such a circulation path could not be continuous (Fig. 1), but probably consisted of a series of eddies in which an over-all north-easterly transport of this water type occurred. To the north of New Zealand the distribution of this water type (Fig. 8) and the topography of the surface (Fig. 1) both indicated a flow to the east, but elsewhere further north no eastward flow occurred. The easterly flow to the north of New Zealand may therefore be the major escape path of this water type from the region.

Water Type (3).—This water type was found in concentrations greater than 50 per cent. to the south of a boundary line running from south of Tasmania to the west of the south island of New Zealand (Fig. 9). In the Tasman Sea to the north of this boundary, it occurred in low concentrations (0–30 per cent.) but to the north of New Caledonia and in the northern Coral Sea its concentration was higher (30–45 per cent.). The topography of the 26·80 σ_t surface showed a movement to the east of southern Tasman Sea waters of this type (Fig. 1). In the north, topographies for August–September only were available (Fig. 1) but these showed a westward movement in the vicinity of Fiji. The Antarctic Intermediate waters beneath the 26·80 σ_t surface flow eastwards south of New Zealand and westwards into the Coral Sea in the vicinity of Fiji (Rochford 1960*a*). It is probable therefore that water of type (3) is entrained into the general circulation of Antarctic waters.

(ii) *May to August*

During the winter period surface densities are at a maximum and sinking of surface waters is facilitated. It has been shown above that water type (2) was the dominant type on the 26·80 σ_t surface. The winter distribution of this water type in the Tasman Sea and adjoining regions in the Southern Pacific Ocean could indicate therefore the major sinking regions.

Water Type (2).—This water type showed concentrations greater than 60 per cent. in three regions (Fig. 10, A, B, C). Region A, in which waters were found with properties almost identical with those of type (2), was situated at the eastern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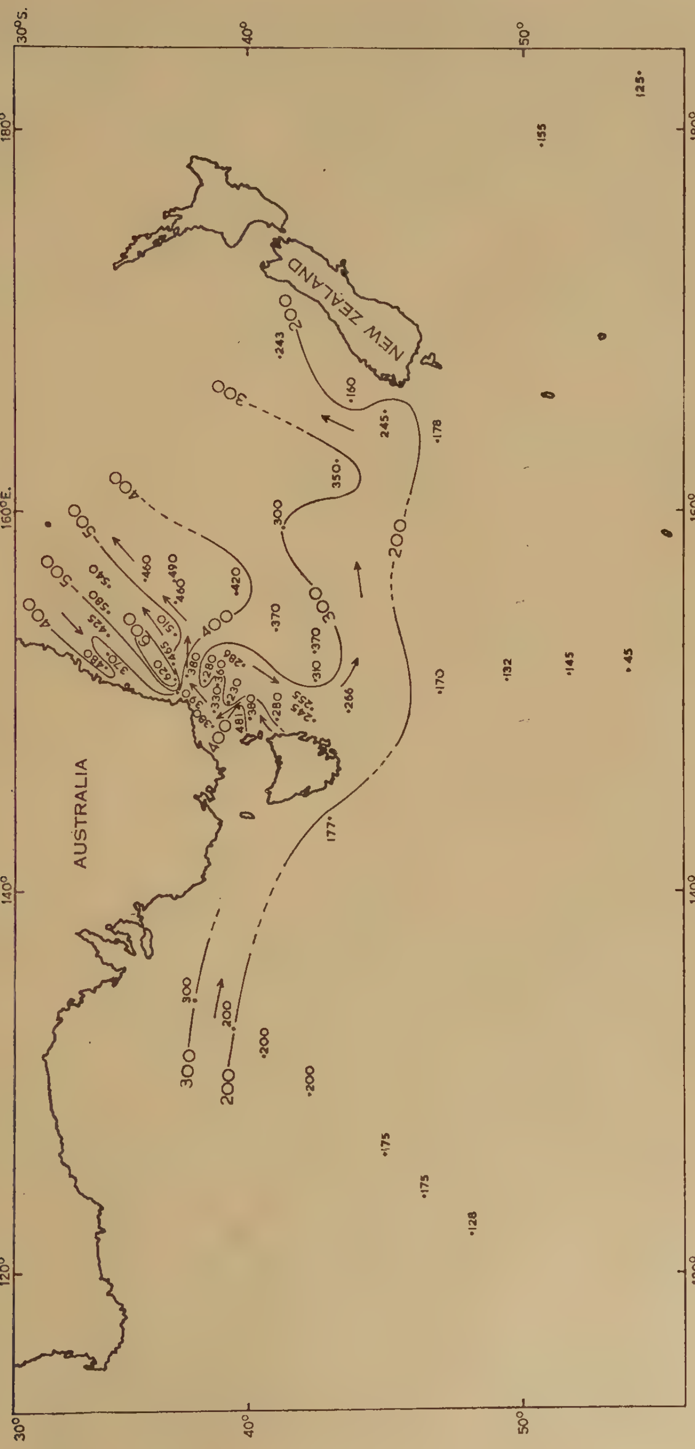
AUSTRALIA
NEW ZEALAND
A
B
C
90
70
60
50
40
30
?

Fig. 10.—Winter (May–August) distribution of the percentage of water type (2). Percentage oxygen saturation values have been circled. The heavy dashed line marks the southern limit of waters containing water types (1) and (2) only.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·540
·580
·425
·480
·370
·510
·266
·177
·170
·132
·145
·45
·155
125·
·200
·175
·128

Fig. 11.—Depth (m) of the 26·80 σ_t surface during winter.

end of the Australian Bight. Region B, in which mixtures of 65–70 per cent. type (2) with 25–30 per cent. type (1) and very little of type (3) were found, was situated north-east of Tasmania and extended north to at least the latitude of Sydney. Region C, in which occurred mixtures of 60 per cent. type (2), 20 per cent. type (1), and only about 10 per cent. of type (3), was found west of the north island of New Zealand. Lack of data makes it impossible to determine the extent of this region or its possible connection with the other regions. In Figure 10 the dashed line separates mixtures of types (1) and (2) in the north from those of types (2) and (3) in the south.

The percentage oxygen saturation values (saturation values for appropriate salinity taken from Figure 6) of waters on the 26·80 σ_t surface (Fig. 10, circled values) were very high in regions A and B, but only 84 per cent. in region C. This implies that A and B are major centres of winter sinking of water type (2), and C a region of its accumulation. The topography of the 26·90 σ_t surface in winter (Fig. 11) shows that water from region A (Fig. 10) flows eastwards probably to southern Tasmania whilst water from region B (Fig. 10) flows north-east along its western and south along its eastern margin. Region C (Fig. 10) could be linked to B by either of these flow paths. In the summer, however, no southern continuity of water type (2) existed (Fig. 8), and it is probable therefore that the northern flow of water type (2) from region B extends eastwards to region C. Region B could thus be the major area of winter sinking of the waters of high salinity on the 26·80 σ_t surface, but further evidence must be sought on the extent of entry of Bight waters from region A (Fig. 10).

TABLE 2

SURFACE PROPERTIES OF WATERS TO THE NORTH OF THE ANTARCTIC CONVERGENCE

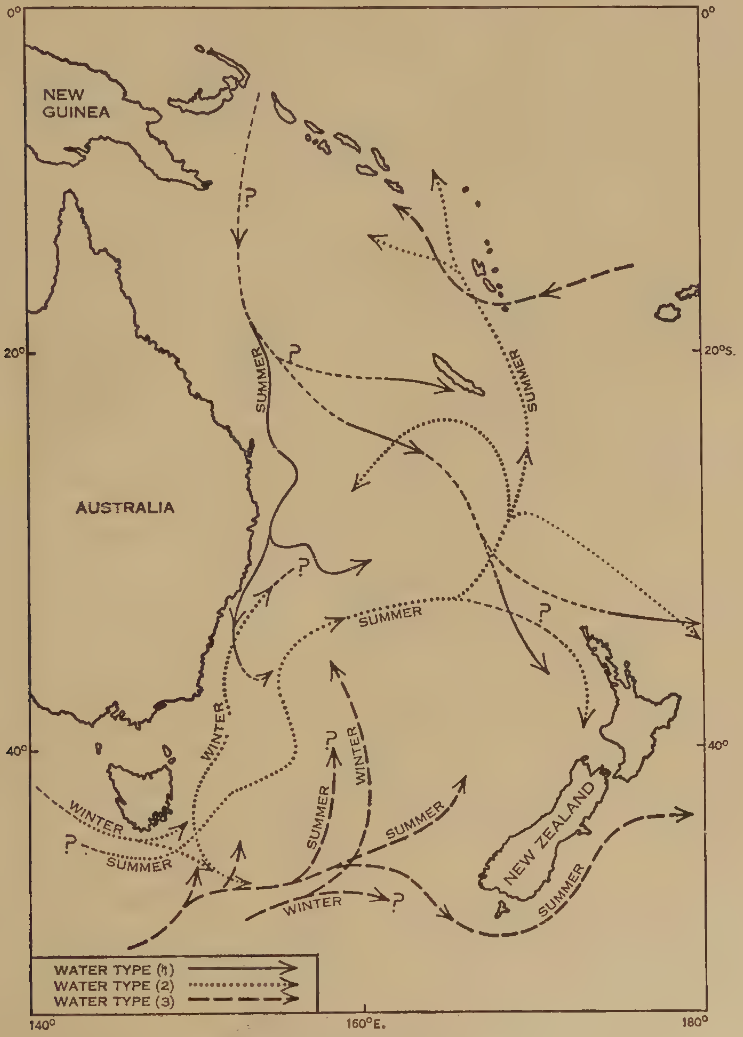
R.R.S. *Discovery* data from Discovery Committee (1941), R.S. *Ob* data from U.S.S.R. Academy of Sciences (1958)

Station	Date	Position		Salinity (‰)	Oxygen (ml/l.)	Phosphate P (μg-atom/l.)
		Lat. (S.)	Long. (E.)			
Discovery 920	26.vi.32	54° 41′	162° 23·1′	33·83	6·97	1·68
Discovery 901	18.vi.32	51° 27·8′	151° 20·5′	33·95	6·61	1·45
Discovery 892	31. v.32	52° 48·5′	137° 0·4′	33·89	6·80	1·60
Ob 69	4.iv.56	54° 14′	159° 46′	33·99	6·82	1·45
Ob 101	6. v.56	51° 1′	117° 10′	33·91	6·94	1·00

(c) *Source Regions and Nomenclature of Water Types*

The waters of type (1) with moderate salinity, very high phosphate, and low oxygen were found near the equator (Fig. 7) in maximum concentration during August and September, and they could have originated in a similar manner to those at deeper levels (Rochford 1960*a*). They are named the Upper Equatorial Intermediate waters (Table 1).

The waters of type (2) with high salinity, high oxygen, and low phosphate are subtropical in character and were found in the central Tasman Sea (Fig. 8) in maximum concentration during summer. During winter even higher concentrations were found to the east and north-east of Tasmania (Fig. 10), but very high concentrations also occurred in the Australian Bight (Fig. 10). Insufficient surface salinities and densities are available to decide the full extent of the source region, or regions, of the high-salinity waters on the $26 \cdot 80$ σ_t surface. These waters have accordingly not been named, but have been given the general description of subtropical (Table 1). It is to be noted that these waters have a much higher salinity than Deacon (1937) found at the Subtropical Convergence (Fig. 6). The waters of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NEW GUINEA
AUSTRALIA
NEW ZEALAND
SUMMER
WINTER
?
WATER TYPE (1)
WATER TYPE (2)
WATER TYPE (3)

Fig. 12.—The major distribution paths and probable circulation of the three water types on the $26 \cdot 80$ σ_t surface.

type (3) with low salinity were of South Pacific Ocean origin (Fig. 9) and occurred at the surface along the northern extent of the Antarctic Convergence south of Australia (Table 2). They form the upper layers of the general movement of Antarctic Intermediate waters into the Tasman and Coral Seas and have therefore been named the Upper Antarctic Intermediate waters (Table 1).

(d) *General Circulation*

Figure 12 combines the information on paths of maximum concentration (Figs. 7–9) and geostrophic circulation for summer and winter (Figs. 1 and 11) into a semi-schematic chart of the general circulation on the $26 \cdot 80\ \sigma_t$ surface. In the Tasman Sea the northern portion of the paths of water types (2) and (3) (Table 1) move about a fixed position off eastern Tasmania, to the west in winter and to the east in summer. The salinities in the central Tasman Sea were much higher in April than in earlier months (Fig. 2). This could mean that the distribution path of water type (2) becomes nearly zonal in position during the autumn period. In the winter, but apparently not in the summer, waters of type (2) (Table 1) move south as well as north from the sinking region B (Fig. 10). The summer distribution paths of water type (1), including an escape path to the north of New Zealand, are based upon isolated occurrences only (Fig. 7). The winter distribution of this water type is not known north of about 30° S.

V. Conclusions

Based upon salinity–phosphate, and to some extent on salinity–oxygen relations, at least three water types must exist to explain the distribution of the properties on the $26 \cdot 80\ \sigma_t$ surface.

(i) An Upper Equatorial Intermediate water type with salinity $34 \cdot 80‰$, oxygen less than $2 \cdot 00$ ml/l., and phosphate P $2 \cdot 50$–$3 \cdot 00$ μg-atom/l. This is found in the equatorial belt to the north of the Coral Sea.

(ii) A subtropical water type with salinity $35 \cdot 20$–$35 \cdot 40‰$, oxygen $5 \cdot 00$–$6 \cdot 00$ ml/l., and phosphate P less than $0 \cdot 50$ μg-atom/l. This originates in the south-west Tasman, but to some extent is continuous with similar waters westwards in the Australian Bight.

(iii) An Upper Antarctic Intermediate water type with salinity $33 \cdot 80$–$34 \cdot 00‰$, oxygen $6 \cdot 00$–$7 \cdot 00$ ml/l., and phosphate P $1 \cdot 40$–$1 \cdot 60$ μg-atom/l. This originates in the South Pacific Ocean to the north of the Antarctic Convergence south of the Tasman Sea and moves north and east in conjunction with the Antarctic Intermediate flow beneath it.

From the relative distribution of these three water types certain conclusions have been derived concerning circulation on the $26 \cdot 80\ \sigma_t$ surface. Subtropical waters entering this surface in the south-west Tasman Sea move north-east to New Caledonia and then north into the eastern Coral Sea. A branch of this movement is directed east to the north of New Zealand and may be the major escapement of subtropical waters from the Tasman Sea. Upper Antarctic Intermediate waters enter the southern Tasman Sea to some extent in both winter and summer, but north of about 35° S. the only possible entry is to the west of the New Hebrides. Upper Equatorial Intermediate waters are entrained into the deeper layers of the East Australian Current and into the deeper circulation of equatorial waters. They are distributed by them in a discontinuous fashion southwards to about 35° S. in the western Tasman Sea with minor drifts into the eastern and south-western Tasman Sea.

The position of the Subtropical Convergence in the southern Tasman Sea has been defined as that region in which the maximum concentration of the subtropical water type, at near saturation oxygen levels, occurred on the $26 \cdot 80$ σ_t surface. The position of this convergence remains fixed off eastern Tasmania, but to the north its position oscillates from extreme west in winter to east in summer.

VI. Acknowledgments

The author is grateful to the Director of the National Institute of Oceanography for permission to use the library of the Institute, and to the Librarian for assistance in extracting data used in this paper.

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SOME ASPECTS OF THE DEEP CIRCULATION OF THE TASMAN AND CORAL SEAS

By D. J. Rochford*

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Summary

Data from selected stations deeper than 2000 m in the Tasman and Coral Seas are used to prepare meridional sections of salinity, oxygen, and phosphate along the meridian 155° E. between latitudes 14° S. and 42° S., and zonal sections of the same properties between meridians 149° E. and 155° E. in the latitude range 14–15° S. Meridional changes in the salinity minimum, phosphate maximum, and deep salinity maximum indicate circulation below 1500 m. Utilizing all available data, the general circulation of these waters in the Tasman and Coral Seas as a whole is described. Phosphate-rich waters from the Equatorial Western Pacific and probably from the Indian Ocean are found distributed along the western margin to the north and south of the region, at about the 2000 m level. Below this level, well-oxygenated waters of high salinity, presumably from the South-West Pacific, enter the northern Tasman Sea, through the New Caledonian trench. By comparison of temperature, salinity, and oxygen values the depth of the sill connecting the Tasman and Coral Seas is estimated at 3000 m. Along the 155° E. meridian temperatures recorded during the late nineteenth century were warmer by $0 \cdot 15$–$0 \cdot 30$°C than those obtained recently.

I. Introduction

Hydrological stations to depths greater than 2000 m are few in the Tasman and Coral Seas. When the *Umitaka-Maru* of the Tokyo University of Fisheries visited Sydney in early 1959, the opportunity was therefore taken to work a line of deep stations through the northern Tasman and Coral Seas (Fig. 1). The study of the data from these stations led to certain interesting hydrological deductions concerning circulation below 1000 m. These results were compared with earlier data collected in the region (Table 1), and they were integrated into a general flow pattern of the water below 1000 m. Wüst (1929), using late nineteenth and early twentieth century data, had prepared a deep meridional section of the western Pacific Ocean, along the line of stations recently occupied by *Umitaka-Maru*. A comparison has been made in this paper of the temperature changes of the deep waters in the 50–60 year interval.

II. Material

Table 1 lists the source of the published station data, and Figures 1 and 2 show the positions of the stations previously worked in this region. Following Wattenberg (1937), phosphate values have been multiplied by $1 \cdot 10$ to correct for salt error. This correction has been applied to the phosphate data of *Umitaka-Maru* and to any uncorrected data from other vessels.

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III. Meridional Section

Umitaka-Maru deep Stations 3 to 19 (Fig. 1) (UM3–19) have been combined with *Dana* Stations 3663 and 3665 (Fig. 2), and *Discovery II* Stations 2728 and 2818 (Fig. 2), to prepare a deep meridional section approximately along the 155° E. meridian.

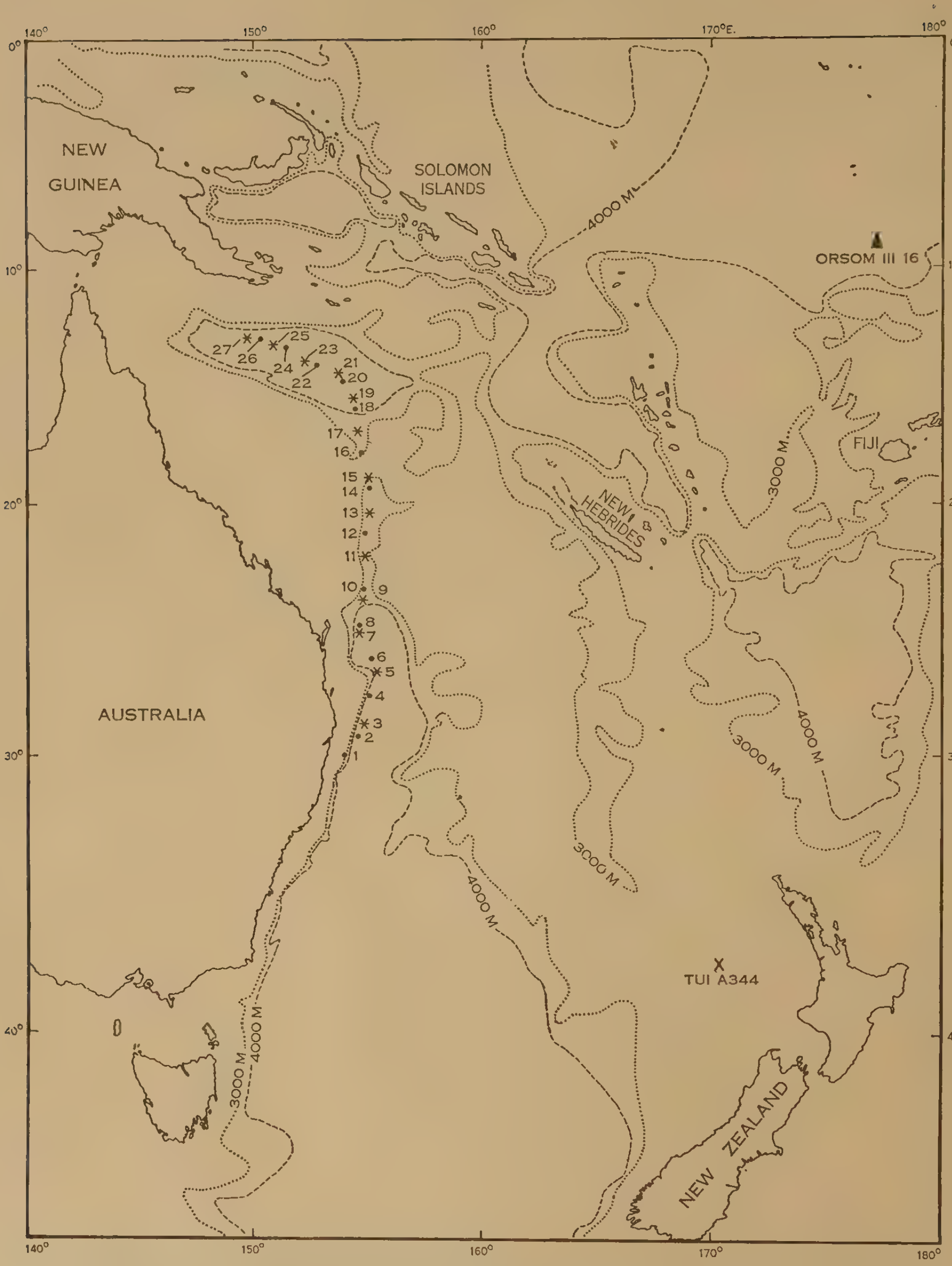
Table 1

PUBLISHED SOURCES OF DATA

Vessel	Station		Reference
	No.	Date	
Albatross	143	3. i.48	Bruneau, Jerlov, and Koczy (1953)
	150	12. i.48	
Dana	3587	2. xi.28	Carlsberg Foundation, Copenhagen (1937)
	3602	22. xi.28	
	3624	10. xii.28	
	3663	23. ii.29	
	3665	25. ii.29	
Discovery II	2727	19. x.50	Great Britain National Institute of Oceanography (1957)
	2728	19. x.50	
	2729	22. x.50	
	2818	23. v.51	
	2819	24. v.51	
	2823	3. vi.51	
Orsom III	16	17. x.56	Rotschi (1957)
Penguin	(*a*)	10. xii.1897	Wüst (1929)
	(*b*)	18.viii.1894	
Satsuma	5	6.viii.56	Japan, Hydrographic Office (1958)
	21	9.viii.56	
	31	17.viii.56	
	38	22.viii.56	
Stranger	17	28.viii.56	Scripps Institution of Oceanography (1957)
	21	29.viii.56	
	28	13. ix.56	
	32	14. ix.56	
	36	15. ix.56	
Tui	A344	14. ii.57	Garner (1958)

(*a*) *Salinity–Temperature*

Figure 3 shows the salinity–temperature distribution along this section. The distribution above 200 m was not plotted because of seasonal and secular effects. The salinity minimum layer was found at 800–1000 m, in association with the 5·00°C isotherm. The value of the salinity minimum ranged from 34·45 to 34·50‰ north of 29° S. to 34·30–34·40‰ south of 34° S. with values greater than 34·50‰ at *Dana* Station 3663. Below 2500 m salinities of 34·70‰ or less were found south of 34° S. and north of 22° S. Between these regions much higher salinities (34·70–34·75‰) were found. The minimum salinity below 2500 m (34·60‰) was found at



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TUI A344
NEW ZEALAND
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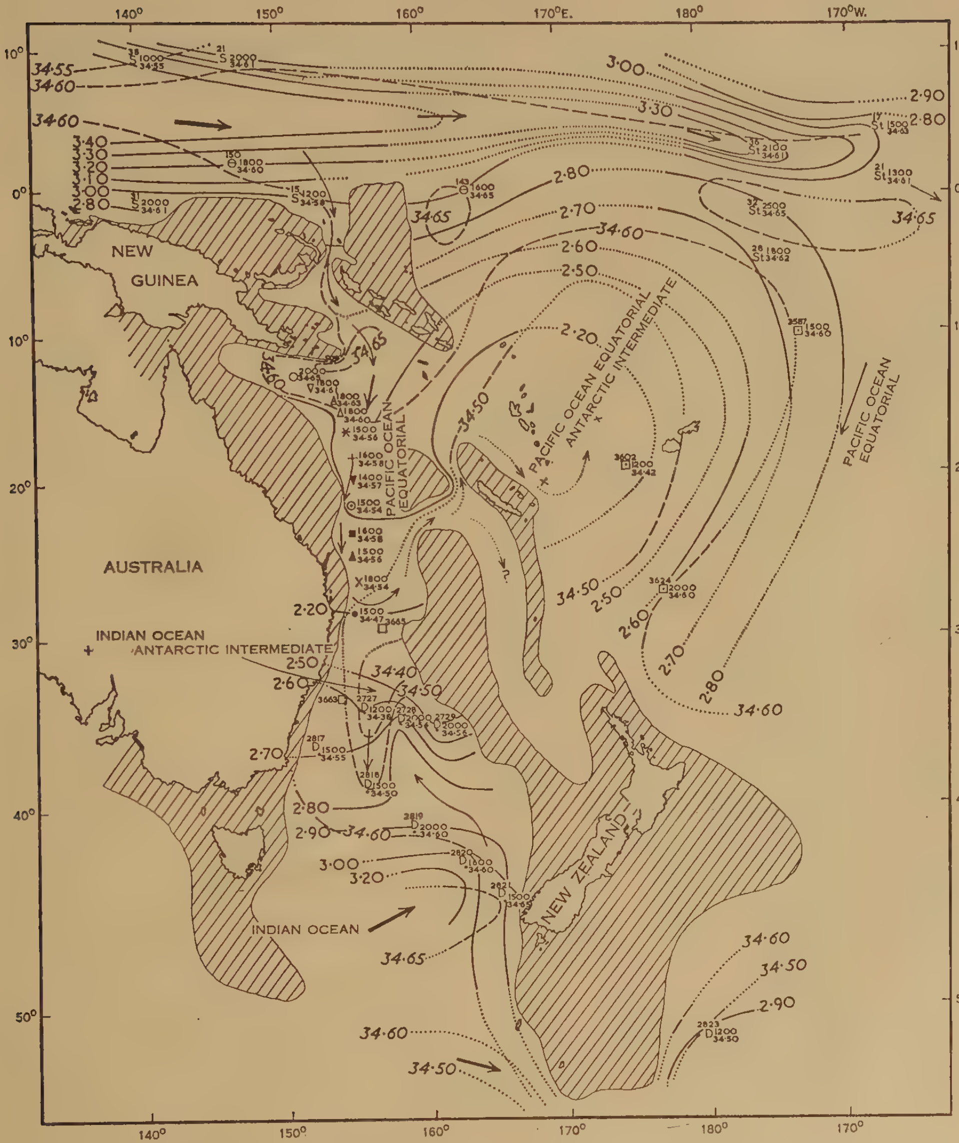
Fig. 1.—Chart of the stations worked by *Umitaka-Maru* in the Coral Sea, January 1959.

● Bathythermograph and surface sample
★ Deep vertical station and bathythermograph
▲ *Orsom III* Station 16
× *Tui* Station A344
.... 3000 m contour
- - - - 4000 m contour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3·10
3·00
2·80
3·00
3·30
2·90
2·80
2·70
2·60
2·50
2·20
34·65
34·60
34·50
34·40
NEW GUINEA
AUSTRALIA
INDIAN OCEAN ANTARCTIC INTERMEDIATE
PACIFIC OCEAN EQUATORIAL
PACIFIC OCEAN EQUATORIAL ANTARCTIC INTERMEDIATE
PACIFIC OCEAN EQUATORIAL
NEW ZEALAND
INDIAN OCEAN
3·00
3·20
2·80
2·90
2·70
2·60
2·50
?
140°
150°
160°
170°
180°
170°

Fig. 2.—Chart of the distribution of phosphates (μg-atom/l.) (upright numerals, line contours) and salinity (‰) (sloping numerals, dashed contours) on the phosphate maximum layer, in the Tasman and Coral Seas. For each station the depth and salinity are given. Full arrows show the major and dotted lines and arrows the proposed secondary flow paths of waters on this layer. Major areas shallower than 2000 m are shown by diagonal ruling. The following symbols identify the stations used:

● UM3
× UM5
▲ UM7
■ UM9
⊙ UM11
▼ UM13
+ UM15
★ UM17
△ UM19
◬ UM21
S Satsuma
▽ UM23
○ UM25
◑ UM27
□ *Dana* 3663: 3665 (1929)
⊡ *Dana* (1929)
⊖ *Albatross* 143–150 (1948)
D *Discovery* 2728 (1951)
D *Discovery* 2818 (1951)
◆ *Orsom III* 16 (1956)
⊗ *Tui* A344 (1957)
St Stranger

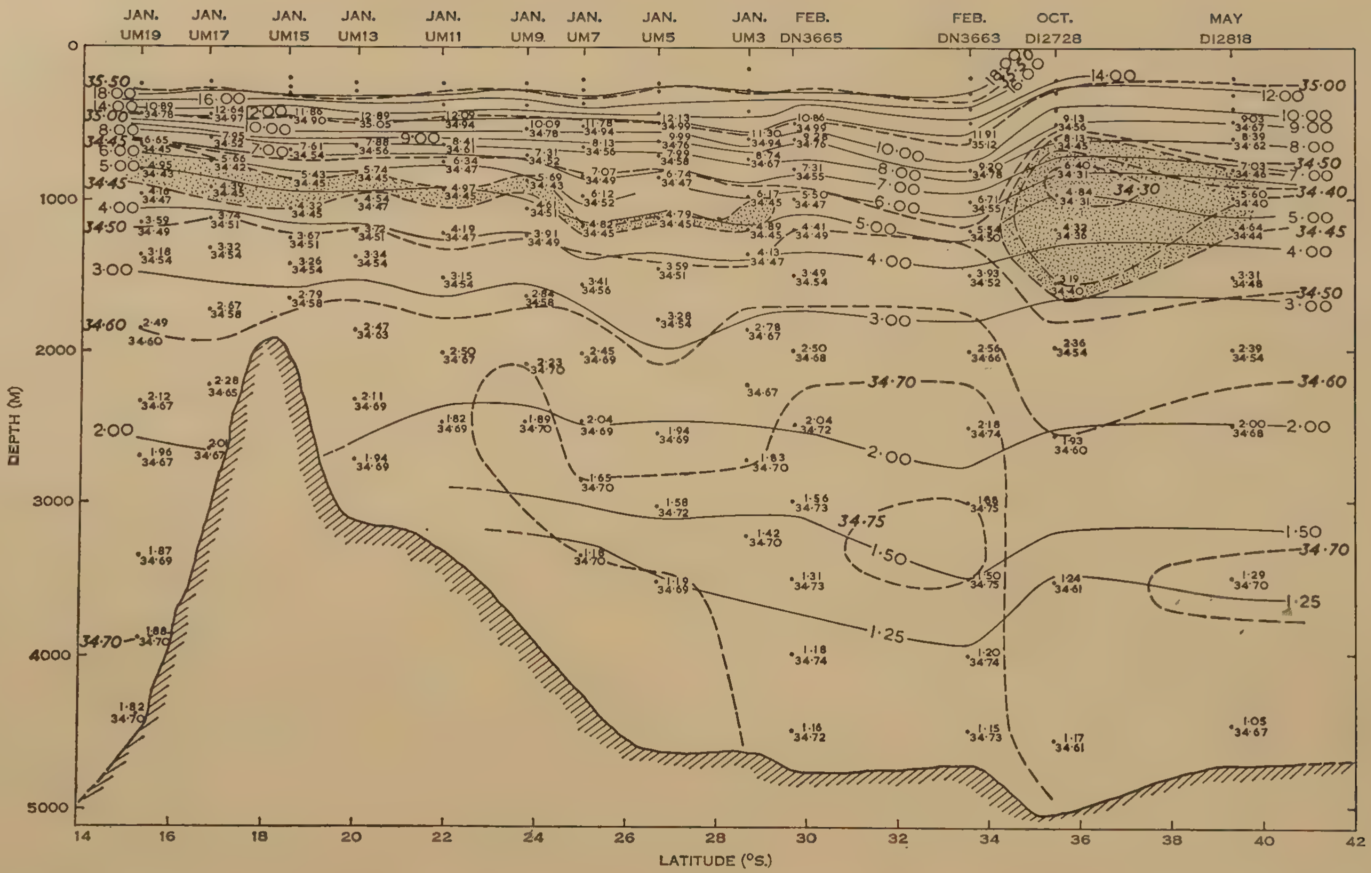

Fig. 3.—The distribution below 3000 m of salinity (‰) (sloping numerals, dashed contours) and temperature (°C) (upright numerals, line contours) at selected stations south of 15° S. The minimum salinity layer is dotted.

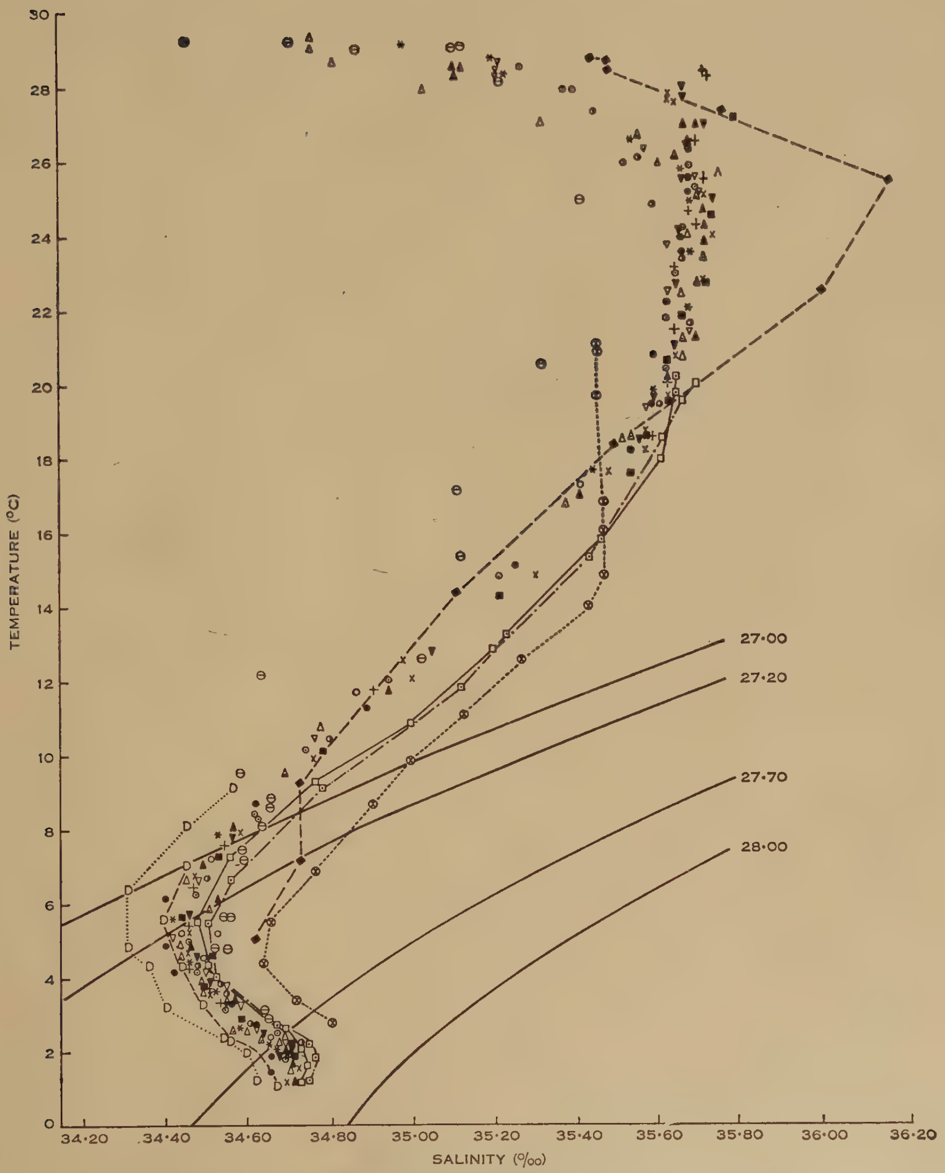

Fig. 4.—The salinity–temperature relations of the *Umitaka-Maru* and selected south-west Pacific station data, identified by the following symbols:

● UM3
× UM5
▲ UM7
■ UM9
⊙ UM11

▼ UM13
+ UM15
✶ UM17
△ UM19
△ UM21

▽ UM23
○ UM25
◑ UM27
□—— *Dana* 3663 (1929)
⊡ ·—· *Dana* 3665 (1929)

⊖ *Albatross* 143–150 (1948)
D · · · · *Discovery* 2728 (1951)
D – – – *Discovery* 2818 (1951)
◆ – – – *Orsom III* 16 (1956)
⊗ - - - - *Tui* A344 (1957)

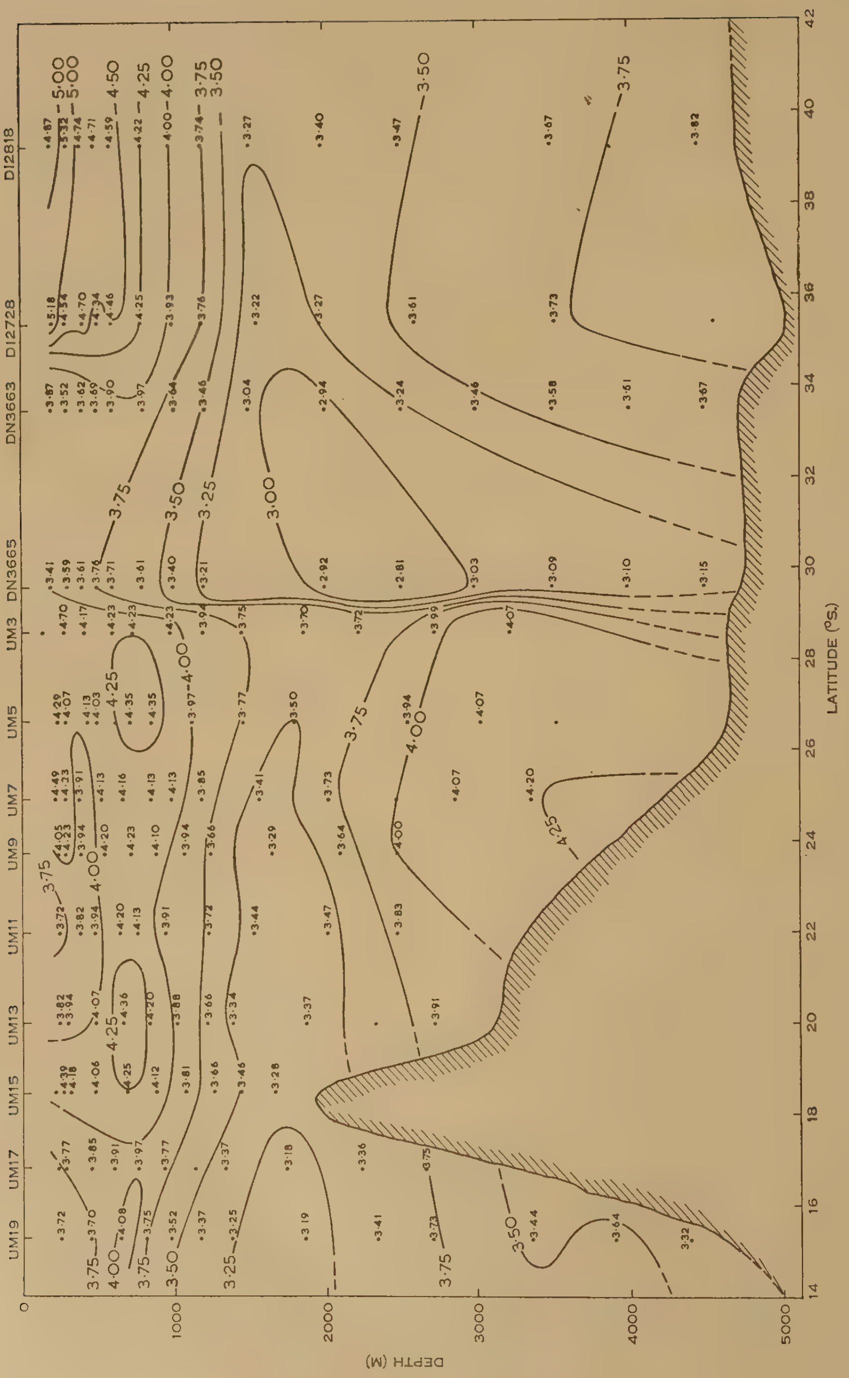

Fig. 5.—The distribution below 300 m of dissolved oxygen (ml/l.) along the section of Figure 3.

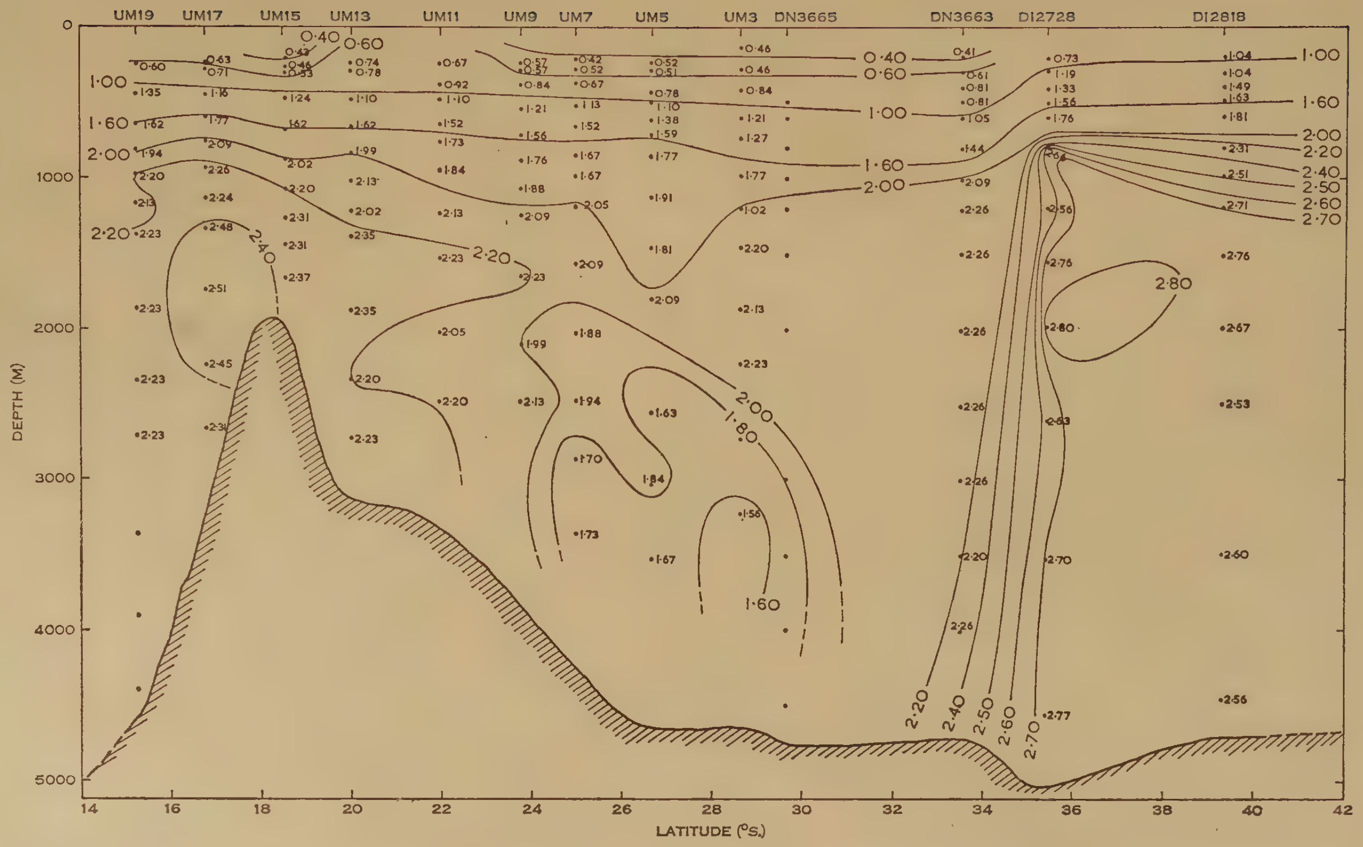

Fig. 6.—The distribution below 300 m of inorganic phosphates (μg-atom/l.) along the section of Figure 3. Values have been corrected for salt error wherever necessary.

Discovery II Station 2728 in 35° S. Temperatures increased southwards below 2500 m, with maximum bottom temperatures in 4500 m at *Discovery II* Station 2728. In the Coral Sea basin, temperatures (Station UM19 only) were 0·50–0·70°C higher below 3000 m than elsewhere. Probably the sill depth for this basin is around the 3000 m level. The salinity–temperature relations of the *Umitaka-Maru* data below a temperature of 24°C (Fig. 4) were very similar from station to station. *Umitaka-Maru* data at temperatures higher than 8°C differed considerably in their salinity–temperature relations from those of the *Albatross* (1948) and *Dana* (1928–29) stations in the area. At lower temperature little difference was found between these two sets of data.

(*b*) *Dissolved Oxygen*

Oxygen values (Fig. 5) increased with depth at practically all stations to a maximum subsurface value just above the salinity minimum layer (Fig. 3). The minimum oxygen values for all depths were found between 1500–2500 m. Below this level oxygen values increased with depth with a maximum at Station UM7. In the Coral Sea basin below 3000 m oxygen values were lower than elsewhere (1929 *Dana* Station 3665 being the only exception).

(*c*) *Deep Circulation*

North of 30° S. a phosphate maximum layer (phosphate P 1·80–2·00 μg-atom/l.) (Fig. 6) was found at depths of 1500–2000 m. South of 34° S. the phosphate maximum layer was not so clearly defined at these depths, and had a much higher value (2·75 μg-atom/l.). The deep waters south of 34° S. had much higher phosphate values than elsewhere.

IV. CORAL SEA SECTION

Deep stations UM19–27 (Fig. 1) have been used to prepare a Coral Sea section running almost east and west through the western half of the Coral Sea basin.

(*a*) *Salinity–Temperature*

The salinity minimum layer continued to rise at the western end of this section and was again associated with the 5°C isotherm (Fig. 7). Salinities below 2000 m were similar to those in the northern Tasman Sea (Fig. 3).

(*b*) *Dissolved Oxygen*

The same vertical distribution as in the northern Tasman Sea was found with high oxygen values (Fig. 8) above the salinity minimum layer (Fig. 7) and minimum values at mid depths (1500–2000 m). The lowest values along this section (3·07 ml/l. at Station UM23) were much lower than the lowest values in the Tasman Sea north of 29° S. (Fig. 4).

(*c*) *Inorganic Phosphate*

The phosphate P values (Fig. 9) within the salinity minimum layer ranged from 1·80 to 2·00 μg-atom/l., and were similar to those in this layer in the Tasman Sea (Fig. 5).

V. Discussion

(*a*) *Circulation of Waters between 500 and 1500 m*

Figure 3 shows that the salinity minimum layer (34·45‰) at the core of the Antarctic Intermediate water was strongly developed south of 34° S., disappeared between 30 and 34° S., and gradually formed again to the north. In the Coral Sea section (Fig. 7) it was also well developed. The core of this layer deepened from about 800 m in the south to 1200 m in the middle of the meridional section (Fig. 3) and rose again in the Coral Sea (Fig. 7) to about 800 m. The core of the Antarctic Intermediate waters south of 34° S. had an oxygen content of 4·25 ml/l. and

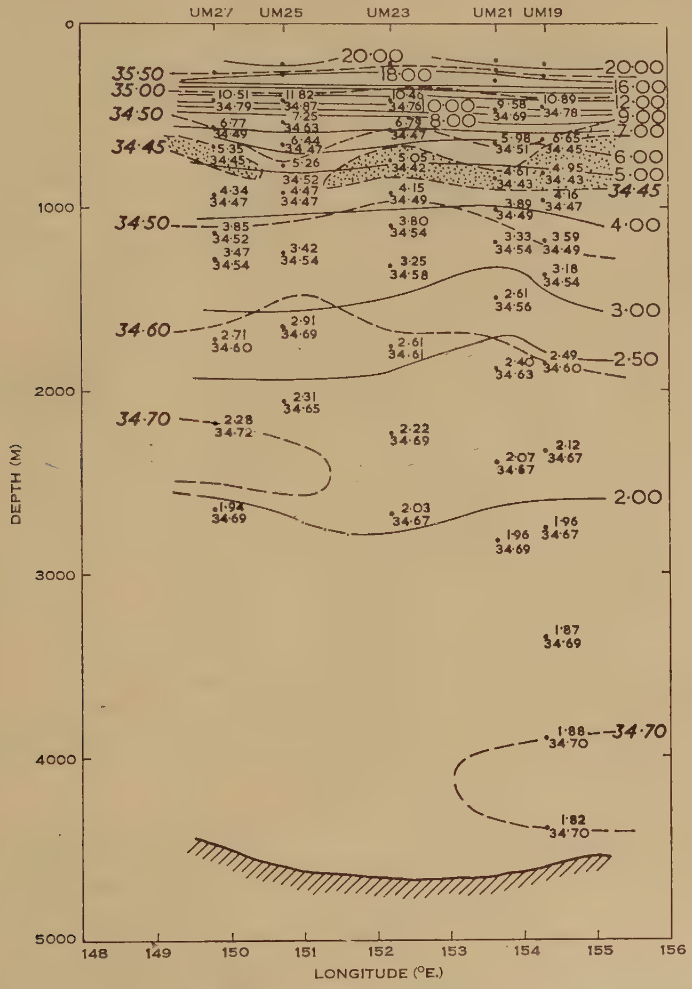

Fig. 7.—The distribution below 300 m of salinity (‰) (sloping numerals, dashed contours) and temperature (°C) (upright numerals, line contours) at selected stations to the north of 15° S. The minimum salinity layer is shown by dotted areas.

phosphate P concentration of 2·00–2·20 μg-atom/l. compared with 3·75 and 1·80–2·00 respectively for those north of 30° S.

Rochford (1959) has shown that the Antarctic Intermediate waters of the Tasman and Coral Seas belong to two separate circulations. The Intermediate waters of the Tasman Sea enter between the 160° E. and 165° E. meridians whilst those of the Coral Sea are part of a general northward flow to the east of New Zealand. A branch of this northward flow diffuses west and enters the Coral Sea around the New Hebrides and penetrates west to its western margin. The differences in properties of the Intermediate waters north and south of 34° S. are probably due to the different age and original surface properties of the waters of these two circulations.

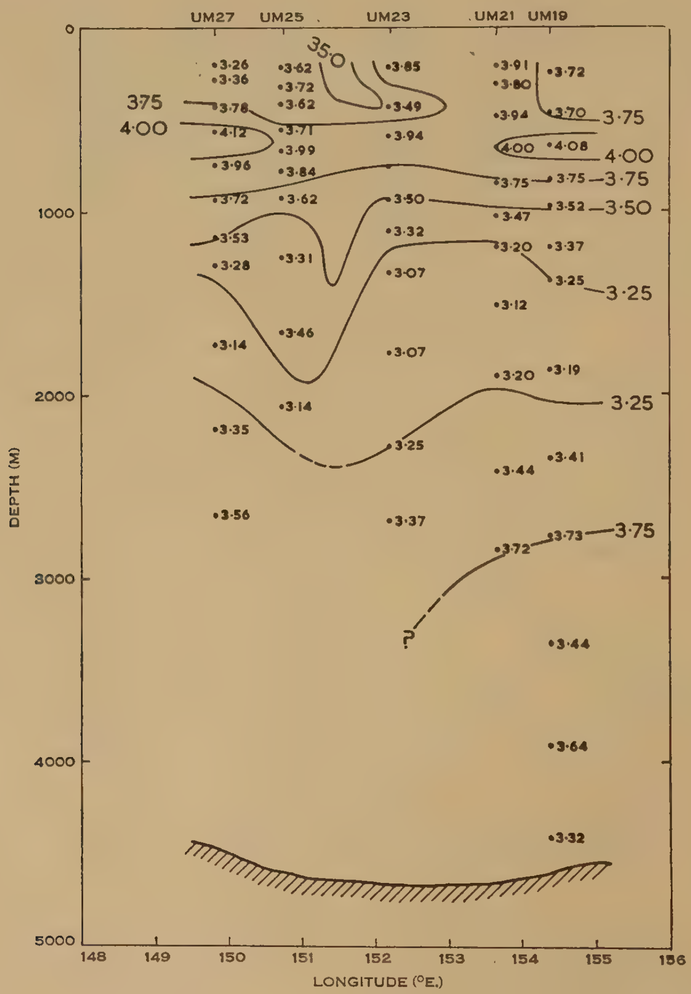

Fig. 8.—The distribution below 300 m of dissolved oxygen (ml/l.) along the section of Figure 7.

(*b*) *Circulation between 1500 and 2500 m*

The phosphate maximum found throughout the meridional (Fig. 6) and Coral Sea sections (Fig. 9) was associated with an oxygen minimum. The origin and circulation of these phosphate-rich waters was examined by charting the absolute value, depth, and salinity of the phosphate maximum layer occurring below the salinity minimum layer throughout the Tasman and Coral Seas. Although the number of stations deeper than 1500 m, in which a definite phosphate maximum occurred, was limited, Figure 2 shows that the phosphate-richest water, and presumably the source of these waters, occurred between 0 and 10° N. at depths of about 2000 m. The main flow of these waters was to the east along the equator, but a branch flow entered the Coral Sea between the Solomon Islands and New Britain.

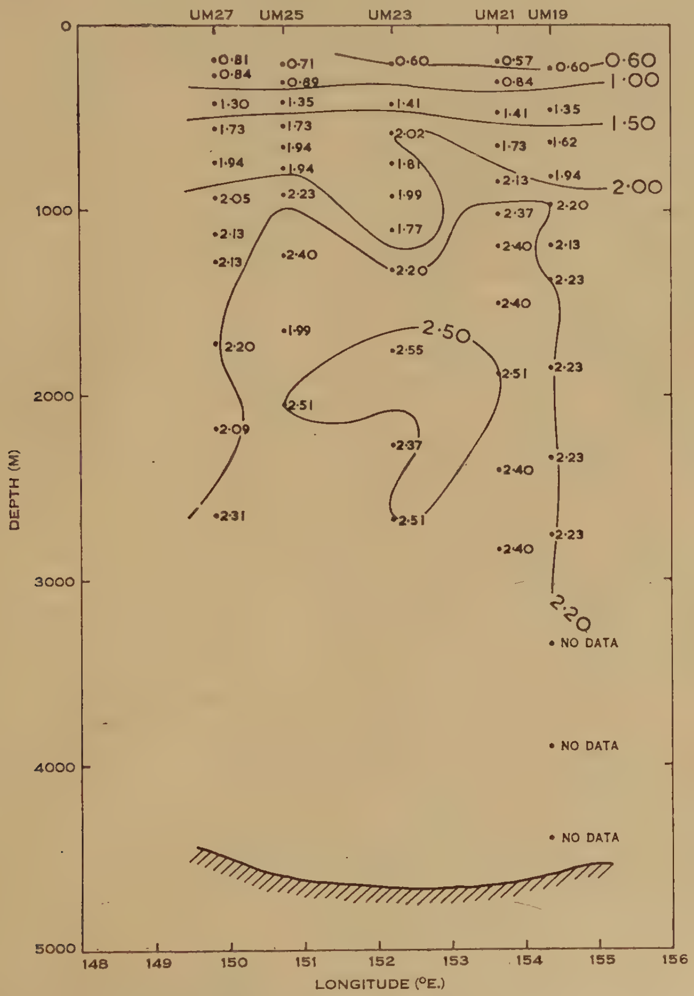

Fig. 9.—The distribution below 300 m of inorganic phosphates (μg-atom/l.) along the section of Figure 7.

These waters then flowed south through the western Coral Sea at depths of 1500–2000 m, and entered the Tasman Sea by the relatively narrow deep channel off the Queensland coast in latitudes 20–22° S. (Stations UM 9–14 in Fig. 1). South of this channel these phosphate-rich waters recurved to the east and north and flowed into the eastern Coral Sea by the deep channel to the west of New Caledonia (Fig. 2). Possibly some flow of these waters to the south also occurred along the New Caledonian trough between the Lord Howe and Norfolk ridges (Fig. 2) (terminology from Brodie (1952)). During their passage from the equator these phosphate-rich waters were mixing with the overlying Antarctic Intermediate water, with consequent decrease in phosphate and salinity values (Fig. 2) and increase in oxygen (Fig. 5). Considering the distribution of the 2000 m contour (Fig. 2) in the Tasman Sea south of 34° S. it is more probable that these phosphate-rich waters were not of Pacific equatorial origin but originated to the west, possibly in the Indian Ocean. These waters apparently moved north along the eastern margin of the Tasman Sea, and by mixing with Antarctic Intermediate waters, lowered their salinity and phosphate values to form the phosphate maximum waters east of Sydney at depths of about 2000 m (Fig. 2). These waters then diffused south along the western side of the Tasman Sea. Despite mixing with Antarctic Intermediate waters these waters of suggested Indian Ocean origin can be distinguished by their much higher phosphate (Fig. 2) and lower salinity (Fig. 2) and oxygen (Fig. 5) from mixtures of Antarctic Intermediate and Pacific Ocean equatorial waters found north of 30° S. (Figs. 2 and 4).

(*c*) *Circulation below 2500 m*

Garner (1958) has given salinity–temperature data for a station in the eastern Tasman Sea (Fig. 1). Compared with other representative stations of the region west of 180° salinities at this station at depths of about 2000 m ($\sigma_t = 27 \cdot 70$, Fig. 4) are much higher. Garner (1958) also stated that these deep high-salinity waters had been traced over a large area of the south-west Pacific, but no data were given. Veronis (1957) has prepared from theoretical considerations a chart of ocean circulation below 2000 m, and has postulated a strong current of South Atlantic waters along the western wall of the Tonga–Kermadec trench to the north of New Zealand. It is possible that a branch of this current curves to the west, south of Norfolk Island, moves south into the southern end of the New Caledonian trough where Garner's station was situated (Fig. 1). It is postulated that these waters flow north from there along the New Caledonian trough and west into the Tasman Sea between Stations UM3 and UM7 where the highest salinities (Fig. 3) and oxygen (Fig. 5) and lowest phosphate values (Fig. 6) were found (3000–3500 m).

(*d*) *Comparison of Temperatures in 1874 and in 1959*

Vertical temperature profiles of stations used by Wüst (1929), in about the same position as the more recent stations (Table 2), are presented here and compared with recent data (Fig. 10). In every case the 2° isotherm was found at about 2500 m. Above this level, deep-water temperatures varied greatly not only during the comparison period but also from station to station. Above 2500 m in the Coral Sea (UM19 and *Challenger* 180, Fig. 10) temperatures were almost identical but were warmer in the deeper layers during the *Challenger* survey. Above 2500 m in the North Tasman Sea (Fig. 10) temperatures were very similar at the comparison stations, UM7 and *Penguin* (*b*) (Table 2). However, no deeper values from the *Penguin* station were available for comparison. Above 2500 m in the South Tasman Sea (Fig. 10) temperatures were very similar at the adjoining stations, *Penguin* (*a*), *Discovery II* 2818, *Challenger* 165*a*, and *Discovery II* 2728 (Table 2). Below this level, however, *Challenger* but not *Penguin* temperatures were higher than recent values. As sufficient data on other suitable properties of these deep waters are absent from the records of the earlier expeditions, it is impossible to establish whether these temperature differences were associated with water mass changes.

TABLE 2

STATIONS SELECTED FOR TEMPERATURE COMPARISON

Vessel	Station	Date	Position	
Penguin	(*a*)	10. xii.1897	41° 21′ S.	153° 59′ E.
Discovery II	2818	23. v.51	39° 21′ S.	155° 36′ E.
Challenger	165a	19. vi.1874	36° 41′ S.	158° 29′ E.
Discovery II	2728	20. x.50	35° 25′ S.	157° 50′ E.
Umitaka-Maru	7	8. i.59	25° 04′ S.	154° 37·6′ E.
Penguin	(*b*)	18.viii.1894	24° 23′ S.	155° 47′ E.
Umitaka-Maru	9	9. i.59	23° 48′ S.	154° 46·5′ E.
Planet	12	28. vi.08	18° 43′ S.	154° 29′ E.
Umitaka-Maru	15	10. i.59	18° 36′ S.	155° 02′ E.
Umitaka-Maru	19	11. i.59	15° 19·5′ S.	154° 19·5′ E.
Challenger	180	24.viii.1874	14° 07′ S.	153° 43′ E.

VI. CONCLUSIONS

(i) Along the western margin of the Tasman and Coral Seas, Antarctic Intermediate waters differed in their salinity, phosphate, and oxygen character to the north and south of latitude about 34° S. These intermediate waters enter the region by two separate routes and the differences in properties are attributed to different source properties and dissimilar aging and mixing changes along their paths of movement.

(ii) The phosphate maximum layer was strongly developed around 2000 m in the western Coral Sea proper and northern Tasman Sea but less pronounced in the Tasman Sea between latitudes 26 and 34° S. This phosphate maximum is thought to be formed by the southward flow of phosphate-rich mid depth waters from the Equatorial Pacific. A mixture of these waters with Antarctic Intermediate waters was traced into the eastern Coral Sea. In the south Tasman Sea phosphate-rich waters probably of Indian Ocean origin were found at depths of 2000 m. These waters were found along the eastern margin of the Tasman Sea and mixtures of them with Antarctic Intermediate waters to the east and south of Sydney along the western margin.

(iii) Below 2500 m, high salinity (greater than 34·70‰), low phosphate P (1·50–1·60 μg-atom/l.), and moderately oxygenated (4·00–4·25 ml/l.) waters were detected in the western margin of the northern Tasman Sea and presumably were part of the flow of high salinity deep waters from *Tui* Station A344 (Fig. 1) and the south-west Pacific in general (Garner 1958). These waters have entered the Tasman Sea along the New Caledonian trench.

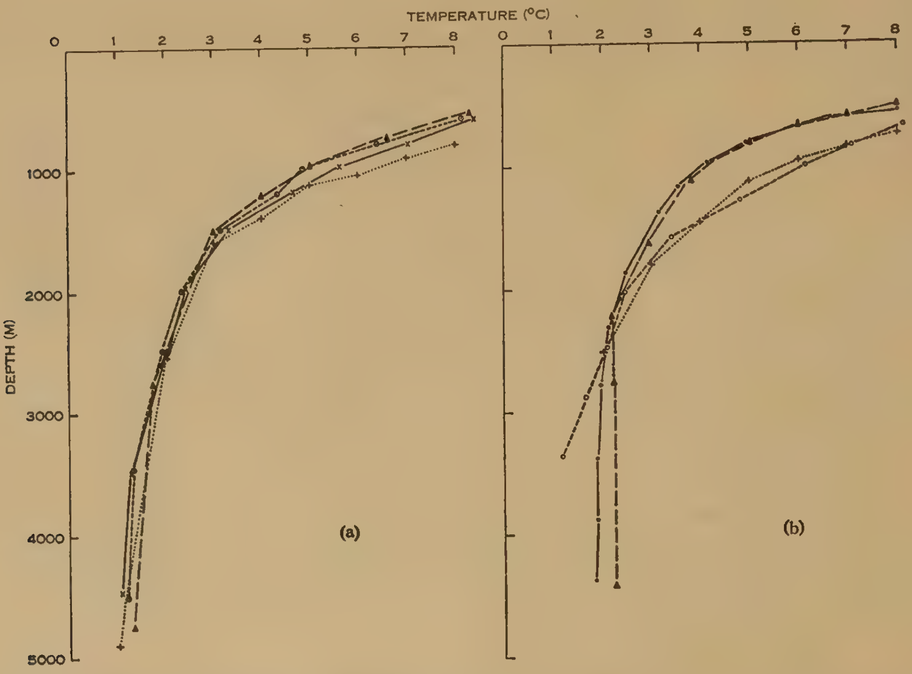

Fig. 10.—Vertical temperature profiles along the 155° E. meridian. (*a*) South Tasman Sea; (*b*) Coral Sea and North Tasman Sea.

Sea	Ship	Station No.	Symbol
South Tasman	*Penguin*	(*a*)	+
	Discovery	2818	×
	Challenger	165a	▲
	Discovery	2728	⊙
Coral	*Umitaka-Maru*	19	●
	Challenger	180	▲
North Tasman	*Umitaka-Maru*	7	○
	Penguin	(*b*)	+

(iv) Below 3000 m the waters of the Coral Sea are higher in temperature, lower in oxygen, and perhaps lower in salinity than the comparable waters of the Tasman Sea. Therefore 3000 m is probably the sill depth of the Coral Sea basin.

(v) Water temperatures below 2500 m were warmer by 0·15–0·30°C during the late nineteenth century than those obtained during this investigation.

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INTERTIDAL ZONATION OF THE EXPOSED ROCKY SHORES OF TASMANIA AND ITS RELATIONSHIP WITH THE REST OF AUSTRALIA

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[*Manuscript received November 9, 1959*]

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Summary

The environmental factors and the zonation of the plants and animals on the exposed rocky coasts of Tasmania are described, and the findings of the present survey are compared with those of other workers both in Tasmania and in south-east Australia generally.

A distinct biota, traces of which were first noticed in Victoria by the present authors (1953), is evident on Tasmanian shores, and the validity of the authors' cool temperate Maugean Province is reaffirmed.

This paper concludes the series of ecological studies (Dakin, Bennett, and Pope 1948; Bennett and Pope 1953) on the intertidal zone of south-eastern Australia.

I. Introduction

Although a number of investigations of the intertidal zone of Tasmania have been published in recent years by Guiler (1950, 1951, 1952*a*, 1952*b*, 1952*c*, 1953*a*, 1953*b*, 1954, 1955), and Cribb (1954*a*, 1954*b*), and references have been made by Fischer (1940), Clark (1946), Chapman (1953, 1957), and Moore (1953), to certain aspects of the biogeography of this region, the field methods and approach in these were not comparable with previous surveys carried out in New South Wales (Dakin, Bennett, and Pope 1948), and in Victoria by the present authors (1953). For the sake of uniformity, therefore, it was felt desirable to survey the coast of Tasmania and the surrounding islands to establish the broad biogeographical relations of intertidal zonation there, with zoning patterns on the mainland of Australia.

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A similar approach has been made in surveys in Queensland undertaken by Endean, Kenny, and Stephenson (1956), Endean, Stephenson, and Kenny (1956), and in South Australia by Womersley and Edmonds (1958).

Guiler (1955) has discussed the biogeography of the Tasmanian intertidal zone with reference to conditions on the mainland. In his papers, however, the south-eastern part of Tasmania only had been dealt with; most of the areas considered range from semi-enclosed bays to still coastal lagoons. Only in a few of Guiler's "transects" are conditions comparable with those ruling in the areas discussed in this paper, or in previous papers which have dealt with surveys made on the mainland. Hence Guiler's biogeographical comparisons between zonation patterns in Tasmania and those of the Australian mainland are not always based on strict analogies. In addition there are apparent inaccuracies in his interpretation of published mainland data.

The present project was planned along lines similar to those of previous surveys, and field methods used correspond with those proved in New South Wales and Victoria. Representative collections were made at each locality. The Mollusca have been placed in the National Museum of Victoria, and the other invertebrate groups in the Australian Museum, Sydney. Algae have been sent to Dr. H. B. S. Womersley (Botany Department, University of Adelaide). Complete lists of species collected at each locality, and distribution maps for all the commoner zoning organisms, are lodged in the Australian Museum.

The 22 localities worked round the Tasmanian coast and a number of the adjacent islands are shown in Figure 1. The only sector not examined was that of the far south-west to which access was impossible owing to the difficulty of transport and lack of time. However, from information which has been collected from many sources, it is not considered that this gap will affect the validity of the general conclusions.

Visits to the west and north-west coasts were made during the summer (January and February) of the years 1954 and 1955; to the north coast during the summer of 1955 (January), and the very late summer (March) of 1958; to the east and south coasts in the winter of 1954 (June), the summer of 1955 (February), and 1958 (March). Seasonal changes were thus observed on the east and south coasts.

Terminology.—Hedgpeth (1957) has endeavoured to clarify the position of terminology in regard to the various marine environments, and Moore (1958, p. 338) quotes for the intertidal area the terminology of Stephenson and Stephenson (1949), which is also used by Southward (1958). Since the latter work is a comprehensive review of the particular zone dealt with here and conditions described fit well those on all the Australian coasts studied by the present authors, its terminology is followed in this paper.

Chapman and Trevarthan (1953) criticized the terminology used by Womersley and Edmonds (1952). The South Australian authors have, however, continued to use it in their 1958 paper even though the Stephensons (see Lewis 1955, p. 287), have pointed out that their universal scheme of intertidal classification, far from failing to apply in South Australia, "fits it like a glove".

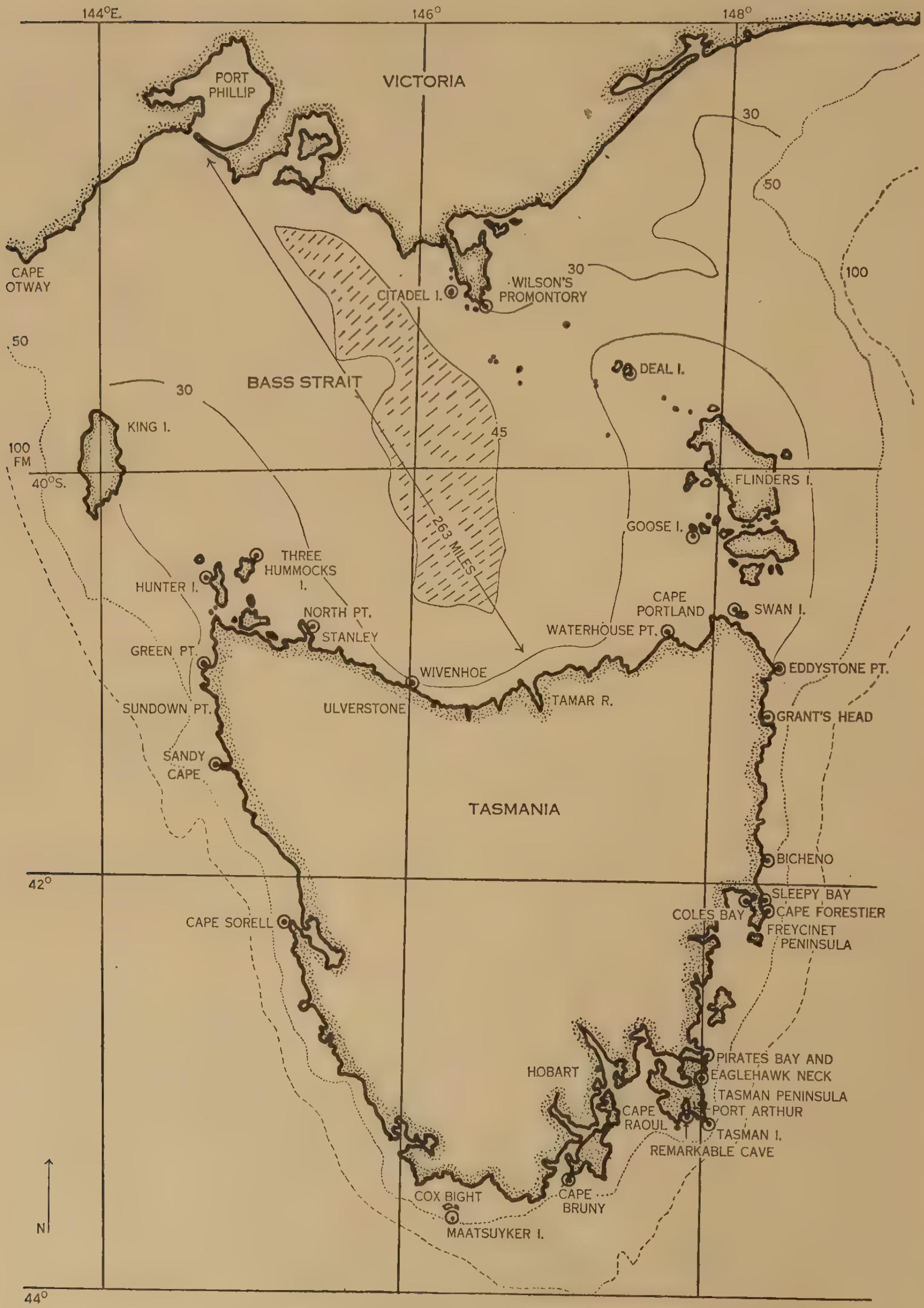
144°E.
146°
148°
PORT PHILLIP
VICTORIA
30
50
CAPE OTWAY
CITADEL I.
WILSON'S PROMONTORY
30
100
50
DEAL I.
BASS STRAIT
30
45
KING I.
100 FM
40°S.
FLINDERS I.
GOOSE I.
263 MILES
THREE HUMMOCKS I.
HUNTER I.
NORTH PT.
STANLEY
CAPE PORTLAND
SWAN I.
WATERHOUSE PT.
GREEN PT.
WIVENHOE
EDDYSTONE PT.
SUNDOWN PT.
ULVERSTONE
TAMAR R.
GRANT'S HEAD
SANDY CAPE
TASMANIA
BICHENO
42°
SLEEPY BAY
COLES BAY
CAPE FORESTIER
CAPE SORELL
FREYCINET PENINSULA
PIRATES BAY AND EAGLEHAWK NECK
HOBART
TASMAN PENINSULA
CAPE RAOUL
PORT ARTHUR
TASMAN I.
REMARKABLE CAVE
N
COX BIGHT
CAPE BRUNY
MAATSUYKER I.
44°

Fig. 1.—Map of Tasmania and adjacent islands showing localities mentioned in the text.

II. The Intertidal Biota

(a) *Environment*

(i) *Substratum*

Following previous surveys on the mainland, work was confined to rocky shores exposed to fully oceanic conditions and to surf, or, where regular surf was absent, as along the north coast, to places where the roughest sea conditions obtained. Enclosed bays and estuaries were ignored. The rocks ranged from smooth, gently sloping, granite outcrops on the northern section of the east coast, through horizontally bedded Permian shales and sandstones along much of the Tasman Peninsula, where rock platforms occur comparable with those of New South Wales, to the very broken shores formed by the jointed and tilted Precambrian and Cambrian quartzites of the west and north-west coasts. Basalts and dolerites formed characteristic promontories and outcrops in several places, as at Stanley and Waterhouse Point in the north, or the southern headlands of the Tasman Peninsula in the south.

Detailed accounts of the geology are to be found in works by Edwards (1941), Hills and Carey (1949), and in a series of papers issued from the Geology Department of the University of Tasmania.

Except where weathering results in the production of shelter-providing boulders, crevices, and pools, the nature of the rocks has been found to have a negligible effect on the broad biogeographical picture as shown in the pattern of zonation.

(ii) *Hydrographic and Climatic Conditions*

Few official data are available which are directly applicable to the intertidal zone. Those available have been published by the Royal Netherlands Meteorological Institute (1949), Guiler (1950 *et seq.*), C.S.I.R.O. Aust. (1951–58), Cribb (1954*a*), Kershaw (1957, 1958), Rochford (1957), and Guiler, Serventy, and Willis (1958).

(1) *Salinity.*—Intensive broad studies have been made of the water masses of the Tasman Sea with regard to their composition and origin by Garner (1954) and Rochford (1957) and in these certain data applicable to Tasmanian coastal waters may be found.

Rochford states that there is evidence of some dilution in the salinity of inshore waters due to drainage of the central highland area of Tasmania after the melting of snow and he recognizes distinct east and west Tasmanian water masses. He provides no information on waters adjacent to the north or south coasts. The temporary dilution referred to above appears to have little permanent effect on the zonation pattern of organisms on the exposed coast. Reference should be made to Rochford's Figures 17 and 18.

(2) *Tidal Range.*—Prior to 1957, no data on tidal ranges strictly applicable to the open coasts of Tasmania were available. Figures quoted by Guiler (1950 *et seq.*), Cribb (1954), and Kershaw (1958) apply to gauges operating in ports and estuaries. As part of the research programme in connection with the Geophysical Year, the Research School of Physical Sciences of the Australian National University, Canberra, established four coastal stations with tidal gauges, and figures

covering a period of slightly more than 12 months are now available from Maatsuyker Island and Cape Sorell, with some readings from Eddystone Point and Eaglehawk Neck. The extreme range for the exposed coasts to date is 5·4 ft, recorded at Eddystone Point, and nearly similar figures (5·1 ft) occur in the west. However, in the extreme south, at Maatsuyker Island, the range is only 4·18 ft.

(3) *Currents.*—Rochford (1957) records the chemical nature and origins of the water masses round Tasmania. The presence of a warm Coral Sea water mass close inshore on the north-east coast in the late summer should be noted, also the fact that Tasmania lies a little to the north of the Sub-Antarctic Convergence.

Some minor tidal currents in Bass Strait were described by Dannevig (1915) who had considerable practical experience in the area. He considered that flood tides entered Bass Strait from both east and west so that the centre of the Strait became a meeting place for these two bodies of water. Tidal streams ebbed back through both ends of the Strait thus creating an oscillating body of water offshore from Tasmania's north coast. How far this affects the sheltered inshore waters of the north coast of the island cannot be gauged from available data, and the area is marked with a question mark in Figure 18 of Rochford's recent work.

Dannevig also postulated a series of minor water movements at the eastern end of Bass Strait. These, together with the westward pressure towards the coast of the warm Coral Sea current in summer, could account for the extension in the range of some warm temperate species from the mainland to the north-east of Tasmania.

The general westerly drift of waters through Bass Strait quoted by Dannevig would also account for similarities in the intertidal populations of South Australia, Victoria, and Tasmania.

(4) *Exposure to Wind and Waves.*—Since confusion has arisen over the question of degree of exposure of certain coasts to wave action, a description is given in Appendix I which may help to clarify terms used in the present work.

Although Tasmania lies in the path of the prevailing westerly winds, according to data given by the Royal Netherlands Meteorological Institute (1949) each of its four coasts shows different wind rose patterns through the year. Consequently their degree of exposure to wave action varies considerably.

On the west coast winds with strong westerly and northerly components blow for much of the year, but it is noteworthy that southerly winds, bringing colder air temperatures, prevail during two of the late summer months (February and March), and also in the winter in June. The intertidal zone of the west coast is exposed during most of the year to maximum surf, and consequently to constant wind-blown spray—a fact which is clearly reflected in the greater width of the zonation pattern.

In the south, which is uninhabited, little information is available for the coastal area proper. Westerlies prevail offshore except in the winter months of July and August when winds are somewhat variable, with slight predominance of north-west elements. This coast also is exposed to rough seas, and may be considered as varying between maximal and submaximal exposure conditions.

No general pattern can be given for the east coast of Tasmania. As may be seen in Figure 1, the southern section of the east coast is a very broken one, and the two peninsulas—the Tasman and the Freycinet—and their offshore islands, have a considerable controlling effect on the degree of exposure to surf, and on local wind patterns. Generally winds are variable, except during autumn and winter when westerly elements clearly prevail. Wave action is for the most part less severe here than it is in the west and the south, and the area can be classified as experiencing moderate to submaximal exposure to seas.

The northern coast is a more sheltered one still, being situated so that it does not experience the same oceanic conditions as obtain round the rest of Tasmania. The island groups at either end of Bass Strait, together with the conformation of the shore, afford some degree of shelter from the westerly winds which prevail in the Strait during much of the year, or from the easterlies which prevail in summer. Along this "sheltered" open shore, winds are variable and the seas choppy, and the absence of regular surf allows some deposition of silt and reduces wind-blown spray in the intertidal zone. This is reflected in the zonation (Fig. 2, column IV).

Taking the wave strength of the Cape Bridgewater area of western Victoria as a standard maximum (Bennett and Pope 1953), it is possible to assess degree of wave action on Tasmanian coasts as follows: the west is constantly exposed to rough seas (slightly less rough than those of western Victoria); the north coast is sheltered from the severest wave action during much of the year, with no oceanic surge; the east coast is exposed to seas which are less rough on the average than those of the west, and also slightly less than those experienced along much of the coast of New South Wales; shores on those parts of the coast facing south are subject to a degree of wave action slightly less than that experienced on the west coast.

(5) *Sea Temperatures.*—Rochford (1957) records a temperature range of 10–17°C for Tasmanian offshore waters. The authors have recorded 10°C in June along the shore, but it is considered that the lowest temperatures would occur a month or two later than this. It follows, therefore, that the lower level of the range of temperature in the intertidal zone may be at least 1 and probably 2°C lower than Rochford's minimum. Kershaw (1957) has recorded 9°C in July on the north coast. Maximum temperature recorded during the present survey was 19°C on the north coast, but in February, 1955, 13°C was recorded at Grant's Head (northern end of the east coast)—a low figure for so late in the summer.

These temperatures are lower by several degrees than those recorded in offshore waters for the mainland of Australia, other than off the Victorian coast (Bennett and Pope 1953).

(6) *Air Temperatures.*—There are no air temperature recordings available which are strictly applicable to the intertidal zone in Tasmania. There are records for some localities near the coast, and these have been quoted by Guiler (1950 *et seq.*), Cribb (1954*a*), Guiler, Serventy, and Willis (1958), and Kershaw (1958). They range from −2°C minimum to 42°C maximum. The latter is, however, highly exceptional.

The data in Table 1 have been taken from figures supplied by the Commonwealth Meteorological Department.

(b) *Zonation Pattern of the Exposed Coasts of Tasmania*

Except for the area on the north coast lying between Cape Portland in the east, and North Point in the west, the patterns of intertidal zonation on surf-washed rocky shores are fairly uniform. The differences observed on the north coast are probably due to consistently calmer seas, and are reflected in the zonation (1) by the absence of some of the surf-tolerant species or those requiring constant wind-blown spray, or (2) by the presence of other species characteristic of moderately sheltered coasts, or (3) by the presence of species tolerant of turbidity in the sea-water. There is a falling-off in numbers of intertidal populations in southern Tasmania, possibly owing to the effect of the colder air temperatures experienced there.

TABLE 1

AIR TEMPERATURE IN °C

Coast and Station	Average Maximum	Average Minimum	Extreme Range
North (Burnie, near the Wivenhoe survey)	15	8·89	−1·11 to 29·44
East (Eddystone Point)	16·5	13	−1·11 to 35
South (Maatsuyker Island)	14	11	−0·56 to 34·2
West (Cape Sorell)	15	9·44	−1·11 to 32·2

The general zonation pattern, and the slight variations to be met with where exposure is submaximal, or even a little less, are shown in Figure 2.

Four major zones are apparent:

(i) *The Supralittoral: Lichen–Littorinid Zone*

Usually three bands may be distinguished in this zone: a band of orange lichen, mainly composed of *Gasparinnia murorum* (Hoffm.) Tornab.; a sooty-black growth; and a littorinid–*Lichina* band.

Rocks above the supralittoral fringe of much of the Tasmanian coast are marked by prominent bands, the upper one a brilliant orange lichen, and the lower band grey-black in colour. The wide orange band is an equally prominent feature along the northern sections of both the east and west coasts, wherever continuous fine spray moistens the rocks. Sporadic patches of bright yellow lichen also occur in some localities. The dark band has not been identified, but could possibly be a blue-green alga. It occurred below the orange and yellow lichens, just above the level where the uppermost littorinids were found.

On the east coast, lichens as a conspicuous wide band have been recorded as far south as the Freycinet Peninsula, and in the west, south to Cape Sorell. This band was missing from the exposed coast south of Eaglehawk Neck and the

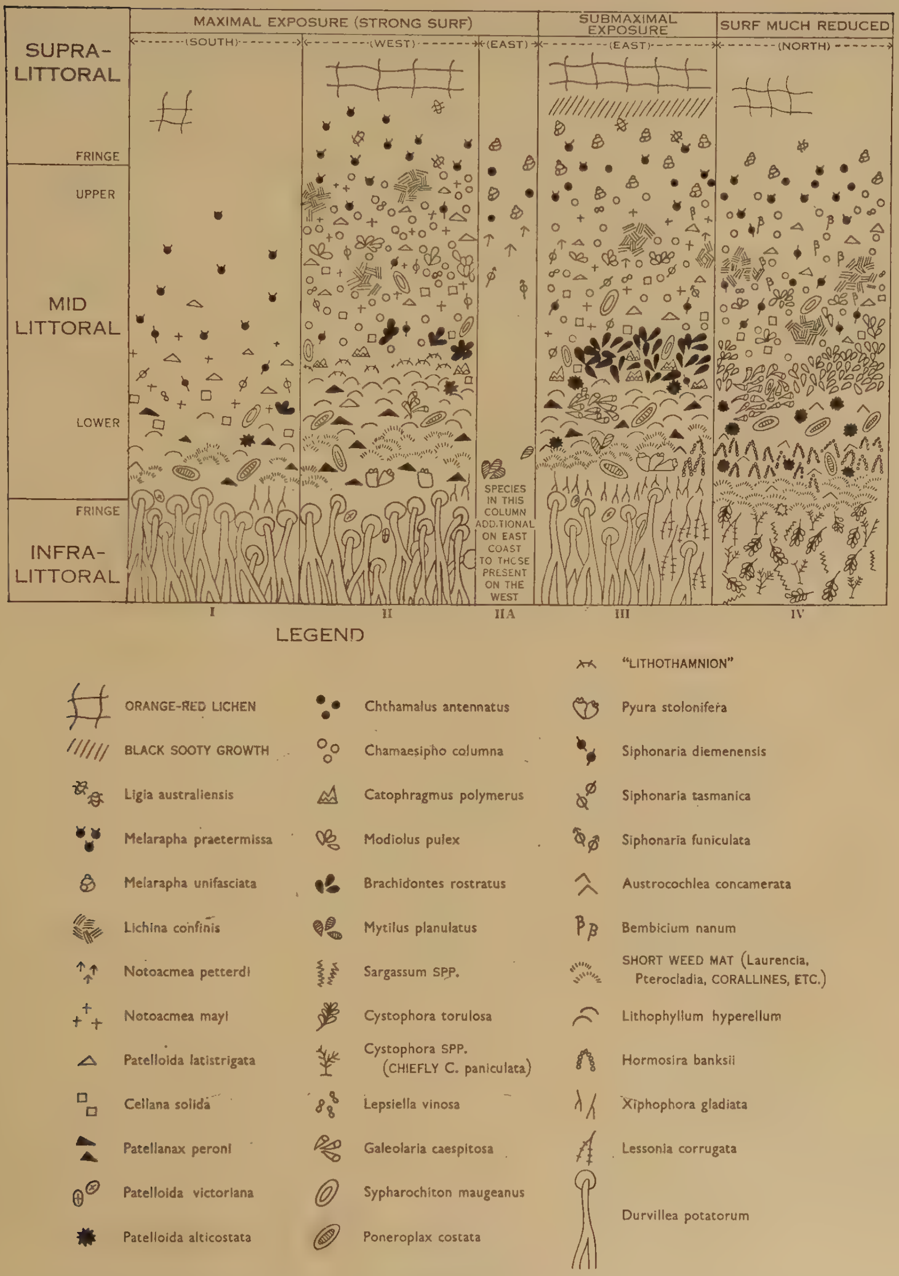
MAXIMAL EXPOSURE (STRONG SURF)
(SOUTH)
(WEST)
(EAST)
SUBMAXIMAL EXPOSURE
(EAST)
SURF MUCH REDUCED
(NORTH)
SUPRA-LITTORAL
FRINGE
UPPER
MID LITTORAL
LOWER
FRINGE
INFRA-LITTORAL
SPECIES IN THIS COLUMN ADDITIONAL ON EAST COAST TO THOSE PRESENT ON THE WEST
I
II
IIA
III
IV
LEGEND
ORANGE-RED LICHEN
BLACK SOOTY GROWTH
Ligia australiensis
Melarapha praetermissa
Melarapha unifasciata
Lichina confinis
Notoacmea petterdi
Notoacmea mayi
Patelloida latistrigata
Cellana solida
Patellanax peroni
Patelloida victoriana
Patelloida alticostata
Chthamalus antennatus
Chamaesipho columna
Catophragmus polymerus
Modiolus pulex
Brachidontes rostratus
Mytilus planulatus
Sargassum SPP.
Cystophora torulosa
Cystophora SPP. (CHIEFLY C. paniculata)
Lepsiella vinosa
Galeolaria caespitosa
Sypharochiton maugeanus
Poneroplax costata
"LITHOTHAMNION"
Pyura stolonifera
Siphonaria diemenensis
Siphonaria tasmanica
Siphonaria funiculata
Austrocochlea concamerata
Bembicium nanum
SHORT WEED MAT (Laurencia, Pterocladia, CORALLINES, ETC.)
Lithophyllum hyperellum
Hormosira banksii
Xiphophora gladiata
Lessonia corrugata
Durvillea potatorum

Fig. 2.—Zoning patterns of the open coast of Tasmania. In columns I–IV it should be understood that within the condition of exposure which heads the column, there is a slight gradation from left to right. The left-hand side of the column represents more severe exposure to surf than the right, owing in the latter case to small local patches that, for one reason or another, are sheltered. Although column I represents largely the zonation pattern of Maatsuyker Island, some orange lichen has been included because of its presence at Bruny Island. (Drawing by F. J. Beeman.)

Tasman Peninsula generally. It was not visible between Tasman Island and Cape Raoul. Cribb (1954*a*), however, records orange lichens within the shelter of Port Arthur, but there they are comparatively inconspicuous. There was a much reduced orange band on the most south-westerly point of Bruny Island, but none at Maatsuyker Island (observation made in midwinter).

In the north, well developed bands were observed on the exposed sides of islands in Bass Strait—Hunter, Three Hummocks, and Deal—visited by one of the authors (I. B.) and on Chappel and Flinders Islands in the Flinders Group (observed by Dr. A. Keast). The absence of a conspicuous lichen band on the north coast between the mouth of the Tamar River and North Point is believed to be due to shelter (see Section II(*a*)(ii)(4)) and the consequent reduction of spray. No marine animals were observed on the rocks at this level.

In the fringing zone of the supralittoral—the area that is washed only occasionally by spring tides—the rock fauna comprised two species of littorinid, *Melarapha unifasciata* (Gray) and *M. praetermissa* (May). Of these, *M. unifasciata* occurred on the east coast of Tasmania and on the islands forming the chain linking Wilson's Promontory through the Flinders Group to the north-eastern tip of Tasmania. Although this species ranges westward along the northern coast, its appearance is sporadic and it was not present on the west coast in any area examined in the present survey. In the south it was recorded from Tasman and Bruny Islands but not from Maatsuyker Island.

Where the two species occurred together, they showed differing habitat preferences. On exposed coasts in the east, *M. unifasciata* inhabitated higher shore levels than the smaller *M. praetermissa*, and was seen on the open surfaces of the rocks. *M. praetermissa*, besides colonizing the lower levels, showed preference for cryptic habitats, favouring crevices, depressions, and areas of rock that were shaded from continuous sunlight (e.g. almost vertical faces). Where *M. praetermissa* was the only high-shore species, as on the west coast and Maatsuyker Island, it colonized the whole rock surface. There sea conditions are constantly rougher, and more flying spray keeps the high back shore moist.

Lichina confinis (O. F. Muell.) Ag. was often found on boulders at this level. Depending on the locality, it sometimes ranges much lower down the shore in Tasmania, being frequently found as small bands or patches on the valves of *Chamaesipho columna* (Spengler) in the upper part of this barnacle's range, and even down to the *Galeolaria* in sheltered areas, as shown by Newton and Cribb (1951, Fig. 3).

The only other inhabitants on these high rock shores were numerous small lizards (skinks), and the isopod, *Ligia australiensis* (Dana).

(ii) *Upper Mid Littoral: Barnacle–Limpet–Mussel Zone*

The mid littoral area on Tasmanian exposed shores has been divided into two subzones only, not three, because the extended vertical distribution of the barnacle, *Chamaesipho columna*, as described below, makes it difficult to see clear demarcation between an upper and a mid region. The mussel, *Brachidontes rostratus*

(Dunk.),* occurs only sporadically and is therefore not considered a suitable indicator for a mid region.

Barnacle populations are smaller in number on Tasmanian exposed shores than on those of the mainland, but barnacles are still dominant species in the upper part of the mid littoral along much of the coast. On the north and east, *Chthamalus antennatus* Darwin and *Chamaesipho columna* occupied the same shore levels as on the mainland. However, towards higher latitudes there was a noticeable reduction in the number of *Chthamalus* on exposed coasts until it disappeared in the extreme south. At Eaglehawk Neck on the Tasman Peninsula it was rare. A few scattered specimens were taken on the extreme north-west coast and offshore islands, but it was by no means a dominant zoning organism, and it was not taken further to the south either at Sandy Cape or Cape Sorell (Fig. 2).

Chamaesipho columna was the dominant cirripede on exposed Tasmanian shores. It covered wide areas of the rocks at, for instance, Sandy Cape, Waterhouse Point, and Bicheno. But between latitudes 42° and 43° S. there was a noticeable thinning out in the number of individuals, even in places where the competition as between *Chamaesipho* with *Chthamalus* (above) and with *Catophragmus polymerus* Darwin (below), ceased to be effective, and *Chamaesipho* had spread to occupy a relatively greater vertical range. In these wider bands its density was, however, still much less by comparison with the mainland, on traverses from high to low water mark.

Catophragmus polymerus occurred sporadically below *Chamaesipho*. It was absent along the sheltered part of the north coast. In the north-west and west it was sparse, despite conditions of exposure to surf which, in New South Wales, would have been considered optimum for this species. On the east coast its occurrence was typical of a species reaching the limit of its geographical range, for where the aspect and temperature were suitable it was present in significant numbers, as at Cape Forestier (Plate 5, Fig. 2), but in less favourable habitats its numbers were greatly reduced. It was sparse on the east coast of the Tasman Peninsula (Plate 6, Fig. 2), and absent from Maatsuyker Island. *Catophragmus* marks the lower limit of the barnacle zone.

As in Victoria, *Catophragmus* may be attached to the mussel, *Brachidontes rostratus*, especially where the latter forms extensive sheets or bands on the rocks and thus excludes the barnacles from the tidal level normally occupied (Plate 4).

In the upper areas of the mid littoral there were numbers of the littorinid, *Melarapha praetermissa*, and a few *M. unifasciata* (within the latter's geographical range), but they were generally juveniles, and their numbers varied according to the season and the stage of their migration up the shore to the levels inhabited by the adults.

It would appear that the same species may play a significant role on two different shore levels at the same time—the juveniles apparently settling on a lower level of the shore at the end of their planktonic stage and only migrating to the upper, more rigorous supralittoral later. It is suggested that there may be an "acclimatization" period during which these animals gradually become accustomed to alternating periods of drying and immersion, since only in the adult, or near-adult stage, is this species found in numbers in the comparatively arid supralittoral. This settlement at a lower level applies also to some other intertidal species, and Moore (1958, p. 372) cites as an example *Purpura lapillus* in the northern hemisphere.

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* Recent systematic work has shown that this is the correct spelling for the genus referred to in all recent Australian literature as *Brachyodontes*. Laseron (1956) has erected a new generic name (*Austromytilus*) for this species but until this receives full recognition it seems best to retain the name used in previous Australian surveys.

The small mussel, *Modiolus pulex* Lam., was frequently found in pockets and crevices in the same area as the barnacle *Chamaesipho*, and in the present survey was found to be common from Cape Sorell in the west right round the north and east coasts to the Tasman Peninsula. On the more sheltered north coast it might even be said to compete successfully against *Chamaesipho* for dominance in the upper mid littoral at some localities. Although always attached to a rocky substrate, the mussels were often embedded in sand (Plate 7, Fig. 2), but the latter is not necessarily a prerequisite condition, as may be seen at Three Hummocks Island (Plate 7, Fig. 1) where there is no trace of sand in the mussel clusters.

Associated with the barnacles, *Chthamalus* and *Chamaesipho*, are the predatory gastropod, *Lepsiella vinosa* (Lam.), and certain limpets and siphonarias. The two latter groups, in Tasmania, assume numerically a more important role in shore zonation than they do in warmer seas, owing to the reduction in barnacle numbers, but whether there is any competition between them and the barnacles can not be determined without experiment. As there appears to be considerable confusion of the species of limpets and limpet-like forms, a diagram has been drawn to indicate the common Tasmanian species, certain of their habitat preferences, and the tidal range they occupy (Fig. 3).

Patelloida latistrigata latistrigata (Angas) was the dominant limpet among the *Chamaesipho* right round Tasmania at every locality worked. In addition, on the east coast as far south as the Tasman Peninsula, and on the eastern chain of Bass Strait islands, a second species, *Notoacmea petterdi* (T. Woods), colonized nearly vertical rock faces. It normally occurs near the inshore limits of rock platforms, and sometimes extends its range even higher than the barnacles into the supralittoral fringe, thus occurring exactly as it does on the south-eastern shores of the mainland. In the present survey, it was not recorded west of Waterhouse Point on the north coast, nor at any of the west coast localities, although Kershaw (1958) states that it is found on the more exposed side of the headland at Stanley.

The largest Tasmanian limpet, *Cellana solida* (Blainv.), reaches the top of its vertical range in this zone. It was found round the bases of large boulders towards the back of exposed shores, whereas on slightly sheltered platforms it ranged down towards the seaward margins of the rocks to the level of the corallines. It occurred all round the Tasmanian coast and adjacent islands.

Another limpet having the upper limit of its vertical range in this zone is *Notoacmea mayi* May, which was found in numbers where the habitat was suitable. It frequented shores where considerable spray was constantly present; thus it was a most prominent species at Cape Sorell on the very exposed west coast (Plate 6, Fig. 1), but on the east coast where surf is less severe than in the west, populations were less, and numbers increased where maximal exposure and spray kept the upper shore moist. In the present survey *N. mayi* was found as far as Maatsuyker Island in the south, but it was not recorded on the north coast between Swan Island in the east and Three Hummocks Island in the west.

Juveniles of *N. mayi* were sometimes found in clusters between *Catophragmus* in the lower part of the barnacle zone (Plate 6, Fig. 2) and they apparently migrate up the shore as they mature (cf. juvenile *Melarapha*). The species is easily distinguished even at this small size because of its shape and the asymmetrical placing of the shell apex (Fig. 3).

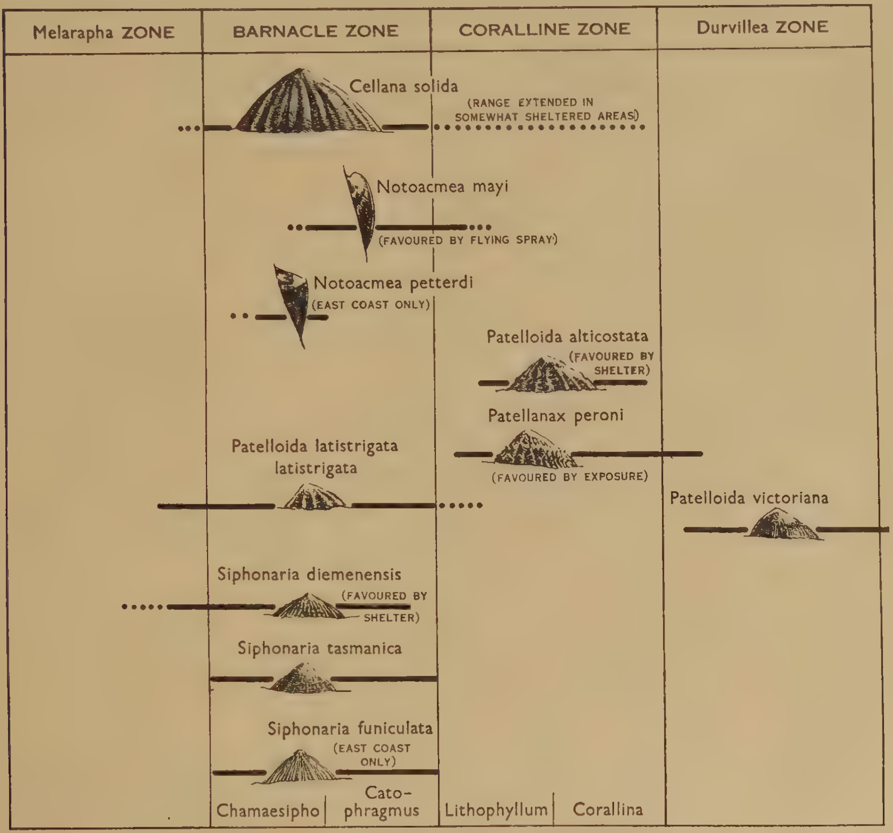
Melarapha ZONE
BARNACLE ZONE
CORALLINE ZONE
Durvillea ZONE
Cellana solida
(RANGE EXTENDED IN SOMEWHAT SHELTERED AREAS)
Notoacmea mayi
(FAVOURED BY FLYING SPRAY)
Notoacmea petterdi
(EAST COAST ONLY)
Patelloida alticostata
(FAVOURED BY SHELTER)
Patellanax peroni
(FAVOURED BY EXPOSURE)
Patelloida latistrigata latistrigata
Patelloida victoriana
Siphonaria diemenensis
(FAVOURED BY SHELTER)
Siphonaria tasmanica
Siphonaria funiculata
(EAST COAST ONLY)
Chamaesipho
Catophragmus
Lithophyllum
Corallina

Fig. 3.—The vertical ranges of the common limpets and siphonarias of the exposed coast of Tasmania are represented by horizontal lines or dots where their occurrence is sporadic. The four major shore zones are represented by the columns. (Drawing by F. J. Beeman.)

Two limpet-shaped pulmonates, *Siphonaria diemenensis* Q. & G. and *S. tasmanica* T. Woods, commonly occurred in the upper part of the barnacle zone, and on the east coast a third species, *S. funiculata* Reeve, was also found (Figs. 2 and 3). *S. diemenensis* occurred on all coasts, frequenting slightly more sheltered conditions, whereas *S. tasmanica* occurred in more exposed areas, being very common on the west coast. It was not, however, recorded at any north coast locality. *S. funiculata* occurs on the south-east coast of the continent and ranges down the east coast of Tasmania, having been recorded between Swan Island and the Tasman Peninsula in the present survey. Also in this zone the chiton *Sypharochiton maugeanus* Iredale & May* occurred at all the areas surveyed.

The mussel *Brachidontes rostratus* is prominent in the barnacle zone in some parts of Tasmania and, as in Victoria, occurs within the vertical range of *Catophragmus*. The species was favoured by moderate exposure to surf, and flat or gently sloping rock surfaces. Only in such places were large beds of mussels in evidence, e.g. Grant's Head, Pirates Bay (Plate 5, Fig. 1), Remarkable Cave, Cox's Bight (from a photograph by A. Hewer), and Sundown Point. Elsewhere, *Brachidontes* occurred only in patches or pockets, or in crevices in exposed areas, but even in such places of sporadic colonization it was sometimes the dominant species, owing to the reduction in the number of barnacles. This was particularly evident in more southerly latitudes, e.g. the south coast of the Tasman Peninsula.

The upper mid littoral carries only a very sparse lichen and algal population. As already mentioned, the dark *Lichina confinis*, in some localities, ranges down among the barnacles, and blue-green algae such as *Rivularia australis* Harv. occur sporadically on boulders among the barnacle *Chamaesipho*. *Ulva lactuca* L. and *Splachnidium rugosum* (L.) Grev., may be found attached to *Chamaesipho*. *Ulva* may also be found in shallow pools along with scattered and stunted *Hormosira banksii* (Turn.) Dec. (Plate 7, Fig. 1). Small patches of *Gelidium pusillum* (Stackh.) Le Jolis occur sporadically, while at lower levels stunted corallines and thin encrusting "lithothamnia" are often found among the mussels or *Catophragmus*. Concentric patches of *Centroceras clavulatum* (Ag.) Mont. sometimes also occur among the barnacles.

Apart from the animals already mentioned above, the following may also be found in this zone:

Coelenterata: *Actinia tenebrosa* Farq., *Oulactis muscosa* (Drayt.)
Crustacea
  Cirripedia: *Tetraclita purpurascens* (Wood), *Ibla quadrivalvis* Cuv.
  Decapoda: *Leptograpsus variegatus* (Fabr.), *Cyclograpsus audouinii* (M. Edw.), *Brachynotus octodentatus* (M. Edw.) (north coast only)
Mollusca: *Austrocochlea concamerata* (Wood), *A. obtusa* (Dillw.) *Melanerita melanotragus* (Smith), *Notoacmea alta* Oliver (on mussels), *N. scabrilirata* (Angas), *Bembicium nanum* (Lam.), *Onchidella patelloides* (Q. & G.), *Kellia australis* (Lam.)† (among mussels)
Echinodermata: *Patiriella exigua* (Lam.)

(iii) *Lower Mid Littoral: Coralline Algal Zone*

The lower mid littoral of Tasmanian exposed shores is characterized by the presence of coralline algae. There may be one, two, or three bands according to the locality and the degree of exposure to surf. On the west coast, the highest is a lithothamnion type of growth which follows the conformation of the substrate and is only a few millimetres in thickness. It appears as though painted on the rock and has a somewhat bleached look. Below this there may be a band of solid encrusting *Lithophyllum hyperellum* Fosli. The boundary between these two growths is not always distinct, for a mosaic-like arrangement with patches of *Lithophyllum* and of lithothamnion occasionally occurs. Below the *Lithophyllum* there is an algal turf in which small mixed species are generally dominated by species of the genus *Corallina*. On the south and east coasts only the *Lithophyllum* and coralline weed mat are present whilst on the north only the weed mat is well developed.

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* It is understood that the systematics of this genus are under revision. Macpherson, in May's (1958) revision, has put *S. maugeanus* into the synonymy of *S. pelliserpentis* Q. & G. of which it can only be reckoned as a subspecies.

† *Lasaea australis* Lam. of previous papers.

Dense growths of the serpulid worm *Galeolaria caespitosa* Lam. were not developed on exposed coasts of Tasmania as they are on the mainland. *Galeolaria* was observed to develop thick encrustations only on the more sheltered rocks of bays and estuaries, but, provided there were suitable rock faces available which did not receive the full force of the waves, it sometimes occurred on the open coast in thinly encrusted bands, having been recorded at such widely distant points as Sleepy Bay, Three Hummocks Islands, and Waterhouse Point. However, its place on the open coast of Tasmania is generally occupied by the coralline *Lithophyllum hyperellum*, which takes the form of raised clumps which are sometimes almost perfect hemispheres. These clumps, when broken apart, are found to shelter a fauna very similar to that usually found within *Galeolaria* clumps on the mainland. This includes isopods, amphipods, tanaids, polychaete worms, encrusting Bryozoa, the tiny bivalve, *Kellia australis*, and juveniles of mussels and of chitons, e.g. *Sypharochiton maugeanus* and *Acanthochiton sueurii* (Blainv.). Dead *Galeolaria* tubes were at times found as the basis of these clumps, obviously killed by an overgrowth of the alga.

Lithophyllum reached its best development on the west coast, obviously being favoured by maximal exposure to surf and flying spray (Plate 1, Fig. 1). It covered a band on the rocks varying in vertical width from 1 to approximately 4 ft, according to slope and aspect with regard to wave action. With increasing shelter, *Lithophyllum* decreased and the turf-like weed mat became more prominent. The fact that *Lithophyllum* was absent from the north coast was attributed again to the relatively sheltered conditions, for it was present at Three Hummocks Island still farther to the north. On the east coast it was sometimes present in exposed places, and a marked feature of the zoning, but the growths were never dense like those seen at Cape Sorell and Sandy Cape. *Lithophyllum* occurred from Maatsuyker Island in the south, right to the northern extremities of the east and west coasts, and was a very conspicuous feature of the Tasmanian intertidal.

Below the Lithophyllum was an algal turf in which *Corallina officinalis* L. and *C. cuvieri* Lamx. were dominant and, sometimes with *Jania fastigiata* Harv., formed the bulk of the weed mat. The following species were found associated with the corallines:

Bryopsis gemellipara J. Ag., *Leathesia difformis* (L.) Aresch., *Adenocystis utricularis* (Bory) Skott. (on the west coast this species occurred among the algal "turf" but at Eaglehawk Neck on the east coast it was found superimposed on the *Lithophyllum*), *Halopteris* spp., *Lophurella periclados* (Sond.) Schmitz., *Ballia scoparia*

Harv. (often with *Chaetomorpha darwinii* (Hook.) Kuetz. epiphytic on it), *Champia tasmanica* Harv., *Pleonosporium comatum* (J. Ag.) de Toni, *Plocamium angustum* (J. Ag.) H. & H., *Centroceras clavulatum* (Ag.) Mont., *Pterocladia capillacea* (Gmel.) Born. & Thur., *Laurencia elata* (Ag.) Harv., and *Ulva lactuca* along the upper limits of the weed mat. This list is by no means exhaustive, comprising only the more common species present. On the exposed south coast of the Tasman Peninsula, *Lophurella periclados* occupied the area which elsewhere was characterized by the mixed coralline weed mat, and was a distinctive feature of this region.

Where there were deep pools and crevices at this level, species of *Caulerpa* *Codium*, and *Cystophora* were common, sometimes with the addition of species such as *Sargassum vestitum* (R. Br. ex Turn.) Ag. Most commonly occurring were *Caulerpa brownii* Endl. and *C. sedoides* (R. Br.) Ag.; *Codium pomoides* J. Ag. and *C. fragile* (Sur.) Hariot, subsp. *tasmanicum* (J. Ag.) Silva; and *Cystophora xiphocarpa* Harv., *C. subfarcinata* (Mert.) J. Ag., *C. spartioides* (Turn.) J. Ag., and *C. torulosa* (R. Br.) J. Ag.

The algal turf reached its best development on the west coast at places like Sandy Cape (Plate 2, Fig. 1), Cape Sorell, and the islands offshore to the north-west. On the east and south coasts it was poorly developed or reduced to a very narrow band (Plate 2, Fig. 2).

The dominant animal species of the lower mid littoral were molluscs—the chiton *Poneroplax costata* (Blainv.) and the limpet *Patellanax peroni* (Blainv.)* (see Figs. 2 and 3; Plate 3, Fig. 2; and Plate 4). Although May (1923) listed *Poneroplax costata* as a species from sheltered waters, it should be noted that this error has been corrected in the revision of May's list by Macpherson (May 1958). *Poneroplax costata* is the species frequenting exposed coasts and *P. albida* (Blainv.) is confined to more sheltered waters. The species recorded on exposed coasts in the present Tasmanian survey is the same as that recorded in Victoria (Bennett and Pope 1953) in similar situations. The genus *Poneroplax* has been found to be a reliable indicator for this shore level in places of either maximal or submaximal exposure to wave action (Plate 3, Fig. 2, and Plate 4).

Without doubt, however, the limpet *Patellanax peroni* (Fig. 3; Plate 2, Fig. 2; and Plate 3, Fig. 2) is numerically dominant among the macrofauna of the lower mid littoral occurring on all exposed coasts. It was not recorded in the present survey from localities along the north coast (Fig. 2).

A third mollusc, the limpet *Patelloida alticostata* (Angas), also occurred at this level of the shore all round the Tasmanian coast, being found in somewhat sheltered areas, and occurring not as a zoning organism, but only sporadically in any locality, where depressions, crevices, or pools offered a slight protection from surf. Unlike *Patellanax peroni* it occurred all along the northern coast and was very common at Stanley in the north-west.

Another animal which was present in some localities in the lower mid littoral of Tasmania was the ascidian *Pyura stolonifera* (Heller). It occurred on exposed coasts only in sporadic clumps, fringing the lower limits of the corallines, and not extending below the upper limits of the holdfasts of the giant fucoid *Durvillea* (*Sarcophycus*) *potatorum* Aresch. It must, therefore, be regarded as a species of the lower mid littoral rather than as an inhabitant of the infralittoral fringe, as it is in New South Wales where it ranges down several feet, below the level of extreme low water of spring tides, among the holdfasts of the large brown algae *Ecklonia radiata* (Turn.) J. Ag. and *Phyllospora comosa* (Labill.) Ag. In careful observations at many exposed localitites round the Tasmanian coast no specimens were found among the holdfasts of the *Durvillea* or below them in places where the lower limits of the rather narrow holdfast band were visible.

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* Macpherson (1955, p. 232) has included the mainland *P. squamifera* Reeve, the name used by the present authors in previous surveys, in the synonymy of *P. peroni*.

Only in areas which were somewhat sheltered and subjected to greatly reduced exposure to surf, as at Pirate's Bay on the Tasman Peninsula, were dense growths of *Pyura* seen resembling those which characterize the zonation pattern on exposed shores of New South Wales (Plate 4).

Apart from the animals mentioned above, the following were taken in this zone:

Porifera: Four species of encrusting sponges

Coelenterata: *Oulactis muscosa* (Dray.), *Cnidopus verater* (Dray.), *Anthothoë albocincta* (Hutt.), *Corynactis australis* Hadd. & Duerd.

Vermes: Leptoplanid worm

Annelida
  Polychaeta, Errantia: many unidentified species
  Polychaeta, Sedentaria: *Spirorbis* sp., terebellids

Sipunculoidea: *Phascolosoma* sp.

Ectoprocta: *Electra pilosa* (L.)
Caberea sp., *Catenicellopsis* sp., *Scrupocellaria* sp.
Bicellaria sp.

Mollusca: *Notohaliotis ruber* (Leach), *Scutus antipodes* Montfort, *Montfortula rugosa* (Q. & G.), *Austrocochlea odontis* (Wood), *Dicathais textilosa* (Lam.), *Cominella lineolata* (Lam.), *Cymatilesta spengleri* Perry, *Cymatiella lesueuri* Iredale, *C. verrucosa* Reeve, *Floroconus anemone* (Lam.), *Subninella undulata* (Sol.), *Micrastraea aurea* Jonas, *Clanculus plebejus* Phil.
Ischnoradsia evanida (Sowerby), *Ischnochiton elongatus* (Blainv.), *Haploplax smaragdina* (Angas), *Heterozona subviridus* Iredale & May, *Cryptoplax striata* (Lam.), *Mytilus planulatus* Lam.

Arthropoda
  Cirripedia: *Ibla quadrivalvis* Cuv., *Elminius simplex* Darw.
  Decapoda: *Lomis hirta* (M. Edw.), *Plagusia capensis* (L.), *Halicarcinus ovatus* (Stimp.), *Paramithrax latreilli* Miers, *Pilumnus monilifera* Haswell

Echinodermata: *Patiriella calcar* (Lam.), *P. gunii* (Gray), *Tosia australis* (Gray), *Allostichaster polyplax* (M. & T.), *Austrofromia polypora* (Clark), *Coscinasterias calamaria* (Gray), *Ophionereis schayeri* (M. & T.), *Ophioplocus bispinosus* Clark, *Pachycentrotus australiae* (Agassiz), *Holopneustes* sp., *Mensamaria thomsoni* (Hutton), and two unidentified holothurians

(iv) *The Infralittoral Fringe: Giant Fucoid Zone*

Round the exposed coast of Tasmania the dominant organisms of the lowest shore level are the giant fucoid, *Durvillea potatorum*, and the encrusting bright pink lithothamnion which occurs on all rock faces not occupied by the large holdfasts (Plates 1–3). Observations at many localities showed that the holdfasts of the *Durvillea* were confined to a fairly restricted vertical range of only a few feet—thus forming an infralittoral fringe in its truest sense. This opinion was confirmed by Mr. A. M. Olsen, Division of Fisheries and Oceanography, C.S.I.R.O. (personal communication), who has repeatedly observed this phenomenon in the course of his diving in connection with work on the life history of the crustacean, *Jasus lalandii* (M. Edw.).

On the north coast, however, *Durvillea potatorum* is absent, and the dominant algae of the infralittoral fringe along those more sheltered shores are species of *Cystophora* (chiefly *C. torulosa* and *C. paniculata* (Turn.) J. Ag.) with, occasionally, scattered small plants of such species as *Macrocystis angustifolia* Bory, *Lessonia corrugata* Lucas, and *Xiphophora chondrophylla* (R. Br.) Mont. (Fig. 2).

In deep pools and chines in the more sheltered parts of the supralittoral fringe around the rest of Tasmania, large brown algae such as species of *Macrocystis* (*M. angustifolia* in the north and *M. pyrifera* (L.) Ag. in the south), *Phyllospora comosa*, and *Xiphophora gladiata* (Lab.) Mont. were sometimes found forming dense growths, e.g. at Eaglehawk Neck, Remarkable Cave, Cape Sorell, or Hunter Island (Plate 1, Fig. 2). No offshore beds of *Macrocystis* were seen on the west coast or in the north, though they were observed along the east coast and in the south off Maatsuyker Island.

Where exposure to waves is submaximal and the slope and aspect of the rocks suitable, a band of *Xiphophora gladiata* is seen just above the *Durvillea*, and with increasing shelter and shade, clumps of *Lessonia corrugata* are also found.

The limpet, *Patelloida victoriana* (Singleton), occurs sporadically on the rocks, among the holdfasts of the *Durvillea*, and is usually coated with lithothamnion, so that it is difficult to detect. It is the only macroscopic animal constantly found at this shore level, though the fissurellid *Notohaliotis ruber* (Leach) was occasionally seen on nearly vertical rock faces along the upper margins of kelp holdfasts. The ceaseless, whip-like lashing of the kelp fronds is not conducive to successful colonization of the rocks by any but the most tenacious organisms, and the tissues of the kelps themselves seem to be unsuitable for the settlement of either epiphytic algae or clinging and encrusting forms such as molluscs, echinoderms, crustaceans, hydroids, or bryozoans.

III. Discussion of Findings of Previous Workers in Tasmania

Some discrepancies in the description of the basic zonation, and in nomenclature, will at once be apparent to the reader when comparing the present paper with those of Guiler (1950 *et seq.*), Cribb (1954*a*), and Kershaw (1957, 1958), and explanations are called for on this subject.

(1) When the works of Guiler were consulted, it was not only found that a number of the names used by him for intertidal animals were outdated and, in the case of molluscs, not all according to May's (1921, 1923) check lists as stated, but also that some field identifications, notably of barnacles* and molluscs, were definitely astray. As a result some unusual records of species have been made.

Guiler apparently has failed to appreciate that, in previous publications, the present authors were dealing only with zonation patterns on coasts exposed to the action of surf, unless expressly stated otherwise. Therefore, where zonation in sheltered areas was mentioned (particularly Dakin, Bennett, and Pope 1948, Fig. 3, and Bennett and Pope 1953, Fig. 4) it still applied to oceanic coasts, so that zonation patterns there figured could not be compared directly with those from embayed areas, inlets, estuaries, or other calmer waters in Tasmania, where much of Guiler's work was carried out. Many of his comparisons, therefore, between Tasmanian zonation and that of the Australian mainland are not strictly valid. Also his standard of degree of exposure to wave action is clearly different from that of mainland workers.

Degree of exposure to wave action is not only subjective and difficult to assess, but since it varies so much no two workers will agree about this important factor of the environment. Womersley and Edmonds (1958, p. 222) have encountered this same difficulty. It is only after long experience in reading signs and zoning patterns that reasonably accurate estimates of degree of exposure throughout the year can be made. The authors are in agreement with Womersley and Edmonds as to the extreme roughness of the seas which batter almost ceaselessly on Cape Bridgewater and various other nearby rocky headlands in western Victoria, owing to the tremendously high swells rolling across the Great Australian Bight, even on calm days. These regularly, and on the average, exceed all but storm wave conditions along the east coast of Australia.

It should also be noted that the zones as described in the present work do not all agree in tidal level with those given by Guiler. The ascidian, *Pyura*, is considered by him to mark the upper part of the infralittoral fringe, whereas the present authors consider that *Pyura* on the exposed coast of Tasmania occurs at a higher shore level than it does in New South Wales. It is, therefore, listed here among lower mid littoral species.

Since Kershaw (1958) follows Guiler in this respect, his mollusc shore zones also do not quite parallel those of the present work.

Bearing in mind these general considerations, the following remarks may help to explain differences between the present account of Tasmanian zonation and those of the Tasmanian workers.

Our observations differ from those of Guiler concerning *Melarapha unifasciata* in the supralittoral fringe (Guiler 1953*a*, p. 93; 1955, pp. 142–3). This is certainly not an "ubiquitous" species in Tasmania, and it does not, on the mainland, extend north to the "tropical Barrier Reef area where it frequents mangroves" and climbs trees. A totally different species occupies this last habitat (Dakin, Bennett, and Pope 1952, p. 247). Moreover the species, *M. praetermissa*, along the east Tasmanian coast, occurs with the same habitat preferences and at the same levels as on the mainland, and does *not* normally occur in a band above that occupied by *M. unifasciata*—even at Eaglehawk Neck. Guiler (1951, 1953*a*) failed to record the presence of *M. praetermissa* at Sleepy Bay on the Freycinet Peninsula, although during the present surveys, it was found to comprise at least 40 per cent. of the *Melarapha* population in the supralittoral fringe at this place.

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* Since many samples of Tasmanian barnacles had been sent to the Australian Museum by various Tasmanian naturalists for identification by one of the authors (E. C. P.), a complete re-check was made of the collections and of the identifications supplied, to make certain that she had made no error. None was found.

We are in agreement with Guiler in finding the populations of the barnacle zone of the shore reduced when compared with those of the mainland, both in number of species present, and in actual numbers of animals per unit area. Guiler (1951, p. 65) was at first inclined to attribute the paucity of barnacles on the east Tasmanian shores to the substratum of smooth granite. The present authors, however, have recorded one of the best-developed barnacle zones, with regard to vertical range, numbers of individuals per unit area, and numbers of species, on the smooth granites of the continuously wave-lashed shores of Wilson's Promontory, Victoria (Bennett and Pope 1953). That granite is no deterrent to development of a well-populated barnacle zone in Tasmania may be seen at several places on the east coast as illustrated in Plate 5, Figure 2, which shows a close view of the rocks at Cape Forestier.

Later Guiler did find barnacles colonizing the granite at this shore level (1953*a*, p. 93), so that some other limiting factor in the environment must have been operating.

In the Sleepy Bay area, Guiler (1951, p. 58) recorded as dominant barnacles of the mid littoral: "*Eliminius simplex* Darwin and *Chthamalus antennatus* Darwin". This statement is difficult to understand in view of the fact that *C. antennatus* is rare to sparse in its occurrence here, and a high shore species, and that *E. simplex* is a solitary species and does not, as he stated later (1955, p. 146) occur as a zoning organism forming bands even on the mainland. *E. simplex* settles always on the lower sides of boulders, or at least in dark places under overhanging rocks or in caves between the levels of low water neaps to low water of springs and perhaps even lower. In wide experience of collecting barnacles including all the east, south-east, and south-west coasts of the mainland of Australia, and many localities in Tasmania, the authors have never taken *E. simplex* in any situation other than the above, and it is a relatively rare species. Nor does it occur in exactly the same habitat as *E. modestus* as stated (1952*a*, p. 8). It is believed, therefore, that the dominant mid littoral species at this latitude, *Chamaesipho columna*, was misidentified in the field as *E. simplex*.

In 1953, Guiler found that *Chamaesipho columna* had become "the most common species" but *E. simplex* is still prominently listed with *Chthamalus antennatus*, and the great increase in *Chamaesipho* is put down to recovery and recolonization of the shore by 1953, from a "sort of barnacle destruction prior to 1950" (1953*a*, p. 93). Wholesale disappearances and recolonizations are the rule rather than the exception among barnacle populations in temperate Australian seas so that assessment and descriptions of zonation based on a single season's observation, or even over a period of only one year, are risky.

As an example of Guiler's failure to appreciate the importance of exposure to wave action may be mentioned his listing together species occurring on the oceanic coast with those of sheltered waters, and even estuaries where seawater is diluted by inflow of rivers. Thus (1952*c*, p. 45) he lists together five species as forming the barnacle belt in Tasmania: *Elminius modestus*, *E. simplex*, *Chthamalus antennatus*, *Chamaesipho columna*, and "rarely" *Tetraclita purpurascens*. Of these, *E. modestus* is a still water, or estuarine species; *E. simplex* is so rare that only a very few specimens (under 20) have been collected from Tasmania in spite of a special search for them by one of the authors (E.C.P.); and *T. purpurascens* should not be considered among zoning organisms as the limiting factor for its vertical distribution is not so much tidal level but a need of some degree of shelter from sun. *Catophragmus polymerus* was omitted altogether from the above list in spite of its importance as a zoning organism in more northerly parts of the island. It certainly plays a more important role on both east and west coasts than does *Chthamalus antennatus*.

Apart from Guiler's apparent field misidentifications of certain important zoning species of barnacles in Tasmania, we disagree with many of the remarks he makes about them throughout his series of papers on the Tasmanian intertidal zone (more especially, 1955, pp. 144–6). Also the statement that *Chthamalus antennatus* and *Chamaesipho columna* "are present on all coasts from exposed to sheltered" in New South Wales, is incorrect and is a specific instance of failure to appreciate the fact that only coasts exposed to oceanic conditions were being dealt with in the present authors' previous works.

The situation becomes even more confused when other species of the mid littoral are considered, and particularly so in the case of mussels, limpets, and siphonarias. The small mussel *Modiolus pulex* is not recorded from Tasmania at all by Guiler, in spite of its frequent occurrence (Plate 7). Since he records "*Brachyodontes rostratus*" in many places from the habitat in which *Modiolus* occurs, and "*Mytilus planulatus*" from the "*Brachyodontes*" habitat, it would appear that these species have been wrongly identified in the field.

The same author's remarks about the mussel beds (Guiler 1952*c*, p. 47) are confusing, partly because of his misidentifications which make it uncertain whether his remarks about the mussel beds on the "higher parts of the shore" refer to "*Brachyodontes*" as stated, or to *Modiolus pulex*, and partly also because comparisons cannot be made between conditions found at Wilson's Promontory (second only to Cape Bridgewater area in severity of exposure to wave action) and more sheltered Tasmanian shores. On the Promontory, barnacles completely dominate the zonation pattern (Bennett and Pope 1953, Fig. 4, Column III) with mussels playing a minor role in slightly sheltered areas with the requisite slope of rock.

In regard to limpets, Guiler states (1952*c*, p. 44), that *Notoacmea* does not occur in Tasmania. This is an amazing statement since members of this genus are amongst some of the commonest organisms on the shore. We have recorded *Notoacmea petterdi* in its normal habitat on the vertical faces of rock in the upper mid littoral right down the east coast of Tasmania, in every locality collected, from Wilson's Promontory across the Bass Strait Islands to the tip of the Tasman Peninsula. A second species, *N. mayi*, also plays a very important role on exposed coasts of Tasmania, and is recorded in the present survey from Hunter Island south to Cape Sorell on the west coast, and from Swan Island in the north-east to Maatsuyker Island off the far south-west. On one or two occasions Guiler mentions a *Patelloida cantharus* (Reeve). In May's (1923) list this species is put into the synonymy of *N. mayi*. The species, *N. alta*, is also found all round the Tasmanian coast (on mussels).

The limpet *Cellana solida* of the present paper is referred to by Guiler as *C. limbata*, and he (1954, p. 113) also records *C. variegata* from south and east coasts of Tasmania. May (1923) records *C. variegata* (which is put into the synonymy of *C. tramoserica* by Macpherson (1955)), as rare and small on the east coast, but from wide field experience of juvenile forms of both species, the present authors would query May's record, although it is supported by Kershaw (1958). As previously stated, the northern species was not collected from Tasmania at all during the present survey despite careful searching.

The most important limpet, *Patellanax peroni*, the dominant animal of the lower mid littoral on all Tasmanian open coasts, has been ignored by Guiler at all localities, and it is not even mentioned in his list of important intertidal species (Guiler 1954, p. 113). In his papers in which he discussed the zone in which *Pattelanax* is found, Guiler states that the dominant animal is the pulmonate, *Siphonaria diemenensis*. This may possibly be the case in sheltered, semi-enclosed waters (since *P. peroni* was not recorded in the present work on the sheltered north coast), but it is certainly not so on the open coast. In the present survey, two species of *Siphonaria*—*S. diemenensis* and *S. tasmanica*—each with its own preferred habitat, are recorded from all coasts of maximum exposure round Tasmania, but (except for sporadic juveniles) never from the low tidal level at which Guiler records the former. Since *Patellanax* and *Siphonaria* are so distinct, and their distribution in the field clearly demarcated, it is difficult to understand this omission, or confusion of genera.

Contrary to Guiler's opinion as expressed in his papers, the occurrence of the serpulid worm *Galeolaria caespitosa* is in no way unusual in Tasmania. In fact this species shows the behaviour common to many intertidal animals when nearing the end of their geographical ranges. It is greatly reduced on the open coasts while surviving in sheltered, fully saline waters. Especially confusing are Guiler's remarks (1952*c*, pp. 50–1; 1954, pp. 116–7; 1955, pp. 143–4). Neither in New South Wales, nor in Victoria and Tasmania, does *Galeolaria* occur except as isolated individuals, usually in shallow pools, above the barnacle *Catophragmus*. In our opinion the *Galeolaria* band is to a large extent replaced by the encrusting coralline *Lithophyllum hyperellum* on the open coast of Tasmania, but the word "replaced" is not used here in the sense so often used by Guiler, i.e. followed by—at the next lower level.

Galeolaria is certainly able to withstand exposure to the sun, as is evident in its occurrence in New South Wales where it thrives without any protection from blazing sun (Dakin, Bennett, and Pope 1948, Plate 5, Fig. 2). Its habitat and occurrence along the coast of New South Wales are clearly defined on pages 196–9 and 212–3 of the above paper, from which Guiler (1955, p. 143) has wrongly inferred that *Galeolaria* is "virtually absent from unexposed coasts". It is in fact a prominent growth on piles, harbour walls, and rocks near the mouths of harbours and inlets in New South Wales.

The ascidian *Pyura stolonifera* is again, in Tasmania, a species reaching the end of its geographical range, and many of Guiler's (1955, p. 142) inferences regarding the difference in its behaviour in New South Wales and Tasmania are incorrect. As with *Galeolaria*, *P. stolonifera* also occurs in New South Wales in harbour waters which are fully saline and have some degree of water movement either in the form of submaximal surf or strong currents. Here it is found on wharf piles, walls, and rocky shores at harbour entrances. It is most certainly a temperate species with the centre of its distribution lying between Camden Haven and Ulladulla in New South Wales, and it ranges both north and south in temperate waters from this area.

The only other species of note recorded from this lower tidal level during the present survey was the limpet *Patelloida victoriana*. It was found on both east and west coasts of Tasmania, but is not mentioned at all by Guiler.

In regard to the algae, much the same criticism may be made. Womersley (1956, p. 344) has already drawn attention to some of the inaccuracies in Guiler's work. For instance, Guiler states (1952*c*, p. 45) that *Hormosira* is the dominant alga of the mid littoral in Tasmania. This is incorrect so far as exposed coasts are concerned. If it occurs there at all, it is found only in pools, or in sheltered areas among boulders at the back of the platform, and it is solely in bays and estuaries that the species shows extensive development.

In his 1954 paper (p. 110) Guiler makes some surprising assumptions regarding certain species of algae. Contrary to what he states, there is nothing unusual in the occurrence at South Cape Bay of *Centroceras clavulatum* as a belt-forming species, since it occurs at other places in Tasmania (e.g. Bicheno on the east coast). Also we have recorded a *Xiphophora* band above the *Durvillea* all round the exposed coast. The species is, however, *X. gladiata*—specimens taken from western, eastern, and southern localities having been checked by Dr. Womersley. In the present survey, the species *X. chondrophylla* has only been recorded from the more sheltered north coast.

Guiler's table of the distribution of important intertidal species in Tasmania (1954, pp. 111–4), not only contains zoological inaccuracies (e.g. the siphonophore *Physalia* does not belong under the Ctenophora, nor is it an intertidal animal) but has many omissions and queries. It has clearly been compiled largely from literature records and not from field collecting, and for this reason is not comparable with lists that have appeared in works by other authors dealing with the Australian mainland. For example, the very common shore crab *Leptograpsus variegatus* which occurs right down the east coast of Tasmania, having been taken at every locality worked in the present survey, is not even listed for the east coast. Species which are purely sublittoral (from 40 fm) are listed with intertidal forms. Brackish-water lagoon, estuarine, and sheltered-water species are all included with no indication of habitat preference, and finally, several very important open coast inhabitants (among them species of the genera *Notoacmea*, *Patellanax*, *Lepsiella*, *Dicathais*, and *Modiolus*) are omitted altogether in spite of their being some of the commonest animals of the rocky shores.

(2) Cribb (1954*a*) has given a comprehensive description of the algal vegetation of Port Arthur which has been found to be much more widely applicable in Tasmania

than to the area designated. The zonation of algae described both for the exposed and semi-exposed parts of Port Arthur might, with a few minor reservations, apply round the whole of the Tasmanian coast with the exception of the north which, though somewhat sheltered from surf, is not sufficiently so for Cribb's "sheltered zonation pattern" (loc. cit., Fig. 2) to apply.

One difference between the exposed area of Port Arthur and the open coast is that the "dense submarine forests" to which Cribb refers (loc. cit., pp. 27 and 32) were not observed generally round Tasmania. This was especially so in the case of the *Durvillea* (*Sarcophycus*) association, for the *Durvillea* occupied only a narrow vertical fringe on the ocean coast.

Another difference is that the serpulid, *Galeolaria*, was not so prominent in the zonation of the open coasts as it is in Port Arthur (cf. his Fig. 2, left and centre columns). It should also be noted that his important zoning species, *Xiphophora billardieri* Mont. is the same as that referred to in the present paper as *X. gladiata*.

Cribb's paper gives details of seasonal changes in shore populations and naturally the bias is botanical, whereas there is a zoological bias in the present work. The two are, in this respect, therefore, complementary. A few minor zoological errors should be noted together with one or two more serious mistakes. For instance, the barnacle, *Catophragmus polymerus*, does *not* "frequently grow on the shells of *Mytilus*" as stated by Cribb (loc. cit., p. 24), but it *is* very often found attached to the shells of "*Brachyodontes rostratus*", especially where this latter species forms extensive bands, and thus effectively excludes the barnacles from their normal tidal level on the rocks (Plate 4). Also the remarks about "*Brachyodontes rostratus*" appearing on page 10 of Cribb's paper should rightly be applied to the "small mussel", *Modiolus pulex*.

Since Guiler in his writings obviously confused "*Brachyodontes rostratus*" with "*Mytilus planulatus*", and mistook *Modiolus pulex* for the true *Brachidontes*, these errors in Cribb's paper (in which he followed Guiler's naming) can be corrected by merely substituting the correct name of the mussel. Cribb's record of *Catophragmus* on "*Mytilus*" is the key that clears up much of the confusion in the writings of Guiler on this subject and also explains why Cribb (loc. cit., p. 15) found it hard to reconcile the "vigorous development [of *Mytilus planulatus*] on [vertical] wharf piles . . . with the preference shown on rocky shores [by this species in his Port Arthur Survey] for the more nearly horizontal surfaces". Two species were involved—the true *M. planulatus* on wharf piles, and *Brachidontes rostratus* which showed "preference" for the flatter surfaces of rocks. When this correction is made, no unconformity will be found in behaviour. Where *Mytilus planulatus* occurs on the open coast it does favour steeply sloping habitats. Plate 4 (centre right) shows several specimens among *Pyura* on a vertical rock face, with solid beds of *Brachidontes rostratus* crowded together on the flat top of the rock.

Cribb, in his work, makes no attempt to differentiate between the various limpets but Figure 3 of the present paper should enable one to account for the wide vertical range of limpets shown on Cribb's diagram of zonation in exposed areas of Port Arthur, which clearly records the sum total of the vertical ranges of all limpet species there.

The same author (Cribb 1954*b*) has fully discussed the occurrence of *Macrocystis pyrifera* round Tasmanian coasts. Since this species is a member of the infralittoral zone it lies outside the field of the present survey except in so far as it is an indicator of cooler temperate seas.

(3) Kershaw (1958) further substantiates the conclusions as to the validity of a separate biogeographical entity in Tasmania, which resulted from our Victorian survey. There are, however, a few minor points of difference of interpretation between his paper and the present work.

For instance, workers unfamiliar with Tasmania may find some difficulty in evaluating Kershaw's remarks on exposure to wave action. He talks of the "exposed north coast" in contradistinction to the sheltered bays and estuaries where much of his work has been done. He himself, however, had pointed out in a previous paper (Kershaw 1957), that the "exposed" north coast was not comparable in degree of wave action with the rest of the exposed coasts of Tasmania. This discrepancy accounts for his listing of species such as *Patelloida alticostata* as occurring in "exposed places" (Kershaw 1958, p. 65), whereas the present authors regard it as "favoured by shelter" (our Figs. 2 and 3). It does occur on wave-washed coasts, but only in sheltered pockets. Kershaw's remarks about the fauna at Stanley are somewhat confusing for this same reason. He has also commented on the broad resemblances between the faunas of the "sheltered" areas in the D'Entrecasteaux Channel in the south, and the "exposed" shores on the north coast.

Kershaw's years of mollusc collecting on Tasmanian shores are reflected by his lists which are more complete than ours. It is, therefore, a matter of interest that his findings support the theory of a distinct endemic element in the Tasmanian fauna. One statement in his distribution table is, however, queried since our field findings were directly the reverse of his—namely the listing of the two species of *Melarapha* on the west coast, and the matter of their abundance. The present survey showed that *M. unifasciata* was absent and *M. praetermissa* very much a dominant species.

IV. Comparison of Tasmanian Zonation with That of the Southern Part of the Mainland

The data on which the following comparisons are based are taken from (1) the authors' 1953 publication and their field notes of the survey of the Victorian coast, and (2) from the paper by Womersley and Edmonds (1958) on zonation of the South Australian coast.

In the latter work, descriptions of somewhat sheltered shores (e.g. those in the St. Vincent and Spencer Gulfs) are included together with those which are fully exposed to surf, but in the present comparison the sheltered areas are neglected.

Since Table 2 in Womersley's and Edmond's work does not indicate the relative abundance of their important zoning species and since this information is not given in the text, it has been impossible to make direct comparisons of their zoning patterns with those of New South Wales, Victoria, or Tasmania, and thus to bring out clearly differences or similarities.

The more important points are, however, indicated in the following summary:

(1) Rocks above the supralittoral fringe in Tasmania differ from those of most of the rest of Australia in having a brilliant and, in places, broad band of bright orange lichen (chiefly *Gasparinnia murorum*). Nowhere else are similarly coloured friezes present, but traces of a band (a faint orange band only) may be seen high up on the southern face of Wilson's Promontory or in the extreme south of Western Australia in the vicinity of Albany. Where bright coloured lichens do occur on the back shores of southern Australia, they are generally sporadic, isolated in patches only a few inches or so across, and not the flamboyant and almost continuous friezes seen in Tasmania, which could only be adequately illustrated in colour. Although these lichens grow so high on the shore as to lie in the "no-man's land" between the terrestrial and the truly intertidal area, yet they appear to be favoured by the presence of salt spray and may thus be considered part of the shore zoning pattern.

(2) Although *Lichina confinis* is common to Victoria, South Australia, and Tasmania, in Tasmania it colonizes rocks to a lower shore level than it does on the mainland (cf. Fig. 2 with Fig. 4 of Bennett and Pope 1953).

(3) Both *Melarapha unifasciata* and *M. praetermissa* occur in the supralittoral fringe of the three southern States but the first species is clearly favoured in warmer areas, being dominant in eastern Victoria and in South Australia, whereas *M. praetermissa* is the more important species in Tasmania, being codominant in the east and the only species on the west coast.

(4) The trend of reduction in populations and in numbers of species of barnacles, first noted in Victoria at places where the coldest air temperatures obtained, is carried still farther in the south of Tasmania where, at Maatsuyker Island, no barnacles were seen in the mid littoral, so that the upper shore is extremely bare. Of the six species found on southern mainland shores, one, *Balanus nigrescens*, is reduced in numbers per unit area in Victoria, fails to bridge Bass Strait to Tasmania, but in South Australia is as common as it is in New South Wales (Womersley and Edmonds 1958, Plate 5, Fig. 1). Two other species, *Catophragmus polymerus* and *Chthamalus antennatus*, are so greatly reduced in numbers on the exposed coast of Tasmania, in the south from latitude 43° S., as to be almost negligible factors in the intertidal populations.

(5) Limpets play a more important role in the intertidal zone in Tasmania than they do in New South Wales, Victoria, and South Australia. *Notoacmea mayi* and *Cellana solida* are much more common in Tasmania than on the mainland where they occur in a somewhat restricted area. They appear to be favoured in the cooler area. The common mainland limpet *C. tramoserica* (Sowerby) was not found by the authors south of Wilson's Promontory in Victoria, although a careful search was made for it on intervening Bass Strait Islands and along the north and east coasts of Tasmania. It is the dominant limpet in the three mainland States and its ecological equivalent in Tasmania is the species *C. solida*. The latter ranges north across Bass Strait to Citadel Island (Glennies Group off Wilson's Promontory) in the east and to South Australia in the west, and there are a few specimens from Cape Otway (southern Victoria) in the collection of the National Museum of Victoria. However,

it was not found to be a constant feature of the intertidal in Victoria (Bennett and Pope 1953). It is not recorded for South Australia by Womersley and Edmonds (1958) although both *C. tramoserica* and *C. solida* have been found side by side in South Australia as far west as Point Sinclair (J. Hope Macpherson, personal communication).

(6) The presence of the darker and less eroded form of the chiton, *Sypharochiton pelliserpentis*, to which Iredale and May have given the name *S. maugeanus*, is another difference between the mid littoral populations of Tasmania and the mainland, for it is not found either in Victoria or South Australia. In New South Wales the form known as *S. septentriones* (Ashby), is common but at a higher level (in the upper mid littoral), and it is usually smaller, very eroded, and has girdle scales more strongly ribbed than the Tasmanian form. Juveniles of the darker Tasmanian form occur, in cryptic habitats only, in the extreme south of New South Wales, but this is the only record on the mainland.

(7) In the lower part of the mid littoral another of the differences between Tasmania and the mainland occurs. The serpulid *Galeolaria caespitosa* plays a more important role on the exposed coasts of the mainland than it does in Tasmania where it is confined to sheltered and embayed areas.

A hard coralline, *Lithophyllum hyperellum*, replaces the *Galeolaria* in Tasmania where it occurs in thick boss-like clumps. Where it flourishes actively, *Lithophyllum* has a mustard-yellow growth coating the surface, but becomes whitened and bleached where growth is less intense. This yellow coloured band is most prominent on the west coast. Such a band was not recorded from Victoria or South Australia, although patches of *Lithophyllum* occur in one or two places in Victoria.

(8) The alga *Hormosira banksii* plays a dominant part in the mid littoral on exposed shores in southern Australia generally, but except in very sheltered areas in pools or among boulders well back on the shore, it is absent on Tasmanian exposed coasts.

(9) The simple ascidian *Pyura stolonifera* which is a prominent mainland feature in the south-east in the lowest area of the mid littoral and the infralittoral fringe, is more or less absent from the exposed coast of Tasmania, being confined to small sporadic clumps in certain favourable localities. It occurs in such places at a higher level on the shore than on the mainland. Often the area which it would occupy on the rock in Tasmania is somewhat bare—possibly an effect of the constant lashing of the fronds of the giant fucoid. *P. stolonifera* is absent from exposed coasts of South Australia.

(10) *Ecklonia radiata* is absent from Tasmanian exposed coasts except in extremely sheltered pools.

(11) Two different species of *Cystophora* play important roles in Tasmania and the mainland. *C. torulosa*, a common alga of the infralittoral fringe along the north coast and occurring sporadically in other less exposed parts of the Tasmanian coast, is absent from South Australia. On the other hand, *C. intermedia*, which is absent from Tasmania, plays a minor role in eastern Victoria, and is dominant along the coast of South Australia.

(12) A feature of Tasmanian zonation not found in Victoria or South Australia is the presence of a band of the brown alga *Xiphophora gladiata*. This occurs above the giant fucoid *Durvillea* wherever exposure to surf is submaximal, and associated with it occasionally is *Lessonia corrugata*. These species have not been observed by the authors in Victoria nor are they recorded for South Australia.

(13) The band of the giant fucoid *Durvillea potatorum* which fringes the lowest part of the intertidal zone in Tasmania (except for the sheltered area of the north coast), is similar to that of Victoria, except that the authors consider that the upper limit of the *Durvillea* in Tasmania is higher on the shore than it was in Victoria. Owing to the constant surge of the ocean this is hard to measure, but it was noted that the holdfasts of the fucoid in Tasmania remained above water for much longer periods during low tides than they did in Victoria.

(14) *Durvillea potatorum* and *Macrocystis* which are indicator species of cool temperate waters, are respectively the dominant species of the Tasmanian infralittoral fringe and infralittoral zone proper. They are extremely rare, if found at all, in South Australia west of Robe.

(15) South Australian zonation also differs from that of Tasmania and Victoria and resembles the eastern warm temperate zonation in

the presence of *Amphiroa anceps* (Lam.) as a common component of the coralline weed mat;

the presence of the gastropod *Ninella torquata* (Gmelin), a typically warm temperate species;

the fact that some echinoderms show marked changes in their vertical ranges: in the colder intertidal zones of Victoria and Tasmania, the sea-urchin *Heliocidaris erythrogramma* becomes subtidal whereas it is intertidal in the warmer seas of the Peronian and Flindersian provinces. The sea stars *Nectria ocellata* Perrier and *Austrofromia polypora* (Clark) behave in the opposite way, being intertidal in the cooler seas, and inhabiting deeper waters (where sea temperatures are lower) in the warmer temperate latitudes from which only dredged specimens have been recorded.

There is a remarkable coincidence in the geographical range of these cases of "atypical" behaviour, and it coincides with the area classed here as Maugean.

The differences in the broad patterns of zonation between the exposed shores of Tasmania and those of the mainland have been given to confirm the original hypothesis that Tasmanian shores would show a better development of cool temperate elements in the intertidal flora and fauna than those of Victoria (Bennett and Pope 1953, p. 152). Also there is a great reduction both in size of populations and numbers of species in the south, foreshadowing conditions found in subantarctic regions such as those described at Macquarie Island (Australian National Antarctic Research Expeditions 1956).

Womersley and Edmonds (1958) have criticized the conclusions in the present authors' Victorian paper (1953). In the light of the many new facts presented for the first time by Womersley and Edmonds some explanation is necessary.

When the Victorian survey was published in 1953 only scattered data were available as to the pattern of distribution of the fauna and flora of the South Australian intertidal. These consisted of check lists and some slightly more detailed systematic papers together with the early ecological papers of Womersley (1947, 1948) and Edmonds (1948) describing Kangaroo Island. It was for this reason that the authors adopted, as a basis from which to work, the limits of the Flindersian Region as defined by Hedley (1926).

In rearranging the biogeographical regions of southern Australia to fit the facts which emerged from the survey of the exposed coasts of Victoria, the present authors concluded with a tentative statement that the shores of Tasmania would probably prove to have definite cool temperate affinities since an overlap from this cool temperate biota could already be clearly discerned in Victoria. The Victorian coast as a whole was regarded primarily as an area of overlap between warm and cool temperate, a fact brought out clearly in Figure 5 of the 1953 paper and, on the basis of the facts in the papers on Kangaroo Island published by Edmonds and by Womersley, this region of overlap was extended westward to include Kangaroo Island.

From the facts given in the recent paper by Womersley and Edmonds (1958), the present authors now consider that the area over which warm and cool temperate influences overlap in the State of South Australia should be extended considerably farther to the west of Kangaroo Island. This is not surprising in view of the general trend of the coast along the Great Australian Bight, which runs rather with the parallels of latitude than across them, and the fact that the area must often be subjected to strong winds originating in colder latitudes. The importance of cold air temperatures as a controlling factor on the intertidal fauna has already been stressed. A cool current from the Southern Ocean apparently also bathes the shores during the summer months, thus possibly inhibiting full development of species favoured by warm temperate conditions.

From earlier publications, it was not obvious that important species favoured by cooler waters, such as *Melarapha praetermissa*, *Modiolus pulex*, *Brachidontes rostratus*, *Lepsiella vinosa*, *Dicathais textilosa*, *Mensamaria thomsoni*, or the alga *Splachnidium rugosum* were found intertidally as far westward as has been shown by the recent South Australian survey. In view of their occurrence in this area it is evident that an extension must be made to the western overlap area.

The ranges of the above species are paralleled in their distribution in New South Wales. For instance, *Melarapha praetermissa* occurs sporadically on the southern coast of New South Wales at least as far north as Jervis Bay; *Modiolus pulex* has been recorded at Jervis Bay and *Brachidontes rostratus* has been taken at Warden's Head, Ulladulla; *Splachnidium rugosum* has been taken as far north as Port Hacking by the authors and other workers have recorded it from Newcastle. However, their occurrences in these warmer latitudes are sporadic, they play no significant part in the zonation pattern and they are essentially inhabitants of cooler waters. The sea temperatures as quoted for the western part of the South Australian coast are comparable with those of north-eastern Victoria and southern New South Wales where the eastern area of overlap in the ranges of temperate species lies.

So far as the fauna is concerned, the area of the Flindersian (western warm temperate) region corresponding to the warmer areas of the Peronian (i.e. northern New South Wales and southern Queensland) probably occurs between Albany in the south and Cockburn Sound (Fremantle) on the west coast.

Womersley and Edmonds refer to "great changes" described by Endean, Kenny, and Stephenson (1956) in the Queensland coastal biota between latitudes 25° and 26° S. where the tropical shore zonation is replaced in the south by a warm temperate one. In the east the change from "tropical" to "warm", or "warm" to "cool" temperate faunas is by no means as abrupt as Womersley and Edmonds apparently believe. The boundaries between regions were placed where the overall picture of intertidal zonation was so markedly changed as to be obvious on sight. If distributions of individual species of animals and plants are followed, each species will be found to have its own range irrespective of arbitrary geographical divisions.

V. Conclusions

In view of the markedly differing pattern of intertidal zonation on the exposed coasts of Tasmania from that of most of the rest of Australia, as set out in Sections II and IV above, and the basic affinity of this pattern with those described in southern New Zealand by Knox (1953) and Batham (1958), and in South Africa (Namaqua Province) by Stephenson (1948), the authors reaffirm the validity of the concept of a cool temperate Maugean biota which was tentatively postulated in 1953, and consider that its individuality is such that it is not a subprovince as suggested by Womersley and Edmonds (1958).

Supporting evidence for the present arrangement of provinces and overlap areas may be found in the recent systematic and ecological investigations of other workers, as for instance:

(1) Macpherson (1955), who has recorded the known distribution of the more important Australian limpets. If the purely tropical species are disregarded, the patterns of distribution for limpets in the temperate region fall into five distinct categories: (i) western warm temperate: *Patellanax laticostata* (Blainv.), *Patelloida nigrosulcata* (Reeve), *Notoacmea onychitis* (Menke); (ii) eastern warm temperate: *Patelloida latistrigata submarmorata* (Pilsbry), *Chiazacmea flammea mimula* (Iredale), *Notoacmea petterdi* (T. Woods), the last of which extends into those sections of the Tasmanian coast that are influenced by an extension of the warm Tasman current in summer; (iii) common to both eastern and western warm temperate: *Cellana tramoserica* (Sow.); (iv) common to both warm and cool temperate: *Patellanax peroni* (Blainv.), *P. chapmani* (T. Woods), *Patelloida alticostata* (Angas); (v) cool temperate: *Cellana solida* (Blainv.), *Patelloida latistrigata latistrigata* (Angas), *P. victoriana* (Singleton), *Notoacmea alta* Oliver, *N. septiformis scabrilirata* (Angas), *N. mayi* May, *N. granulosa* Macpherson, and *Chiazacmea flammea flammea* (Q. & G.).

These subdivisions clearly agree with the present hypothesis, and since limpets are so prominent in the intertidal zone, such evidence is important.

(2) Stephenson and McNeill (1955), who doubted "whether south-east Australia can be included in the Indo-Pacific area from the aspect of stomatopod biogeography" and found a small endemic fauna in Tasmania and Victoria.

(3) Wood (1954, p. 329 *et. seq.* and Fig. 264) and Crosby and Wood (1958), who have shown by means of dinoflagellates and diatoms in the plankton that there is a body of cool temperate water round Tasmania and in Bass Strait, and also the presence, at times, of a warm-water microflora west of King Island. In the later work they postulate a warmer water microflora in the offshore waters of New South Wales extending as far south as Eden, and reappearing at Babel Island, off north-eastern Tasmania, after complete absence in the intervening waters, and they suggest that a current anomaly—e.g. vertical mixing—causes this latter distribution.

Indicator species are given in their work for each of these water masses, and it is significant that the species characterizing the warmer east coast waters differ from those characterizing the west wind drift. Thus it is reasonable to expect that there will also be certain differences in the intertidal biotas as well, reflecting the differing origins of the currents bathing the two areas.

(4) Dall (1957) and Racek (1959), who, working on penaeid prawns, have shown that this important commercial group, so far as is known, is absent from southern Victoria and from Tasmania.

Dall states: "A cool-temperate Australian penaeinine fauna is virtually non-existent. Prawns are absent from the cold Maugean Province (as defined by Bennett and Pope (1953)), and *Penaeus latisulcatus* and *Metapenaeopsis novae-guineae* are rare in South Australia and confined to sheltered inlets".

In the later paper, Racek (p. 12) sets out the distributions and the species characterizing the following geographical regions:

"Eastern warm temperate region—
  Lakes Entrance (Vic.) to Cape Moreton (Q.)

Tropical region—
  Cape Moreton to Cape Inscription (W.A.) [between 25° and 26° S.]

Western warm temperate region—
  Cape Inscription to Kangaroo Island (S.A.)."

It should be noted that the two species recorded by Racek in the extreme north-east of Victoria (i.e. in the eastern overlap area) are small populations of the two typical eastern warm temperate species at the extreme southern end of their ranges. Racek also has recorded no penaeids in more southerly waters.

These recent findings, therefore, support very effectively the claim for the presence, in the cooler waters round Tasmania, of a separate Maugean province which overlaps into Victoria and the eastern section of South Australia.

Much of the intertidal fauna of Australia has its origin in the tropical Indo-Malayan area and, as one proceeds farther and farther south into cooler waters, there is consequently an appreciable thinning out in the numbers of species able to survive. This is clearly shown by the distribution of stomatopods, penaeids, barnacles, and crustaceans generally. Owing to the isolation of the southern part of the Australian continent from other land masses, there is little chance of a compensating influx of colder-water intertidal animal species to augment this thinned-out fauna.

In this general trend of reduction of populations, therefore, even a low rate of endemism is significant, especially since sea-current systems in the area tend to favour the spread of warmer water species into the cold areas rather than the reverse.

The following list shows that a considerable degree of endemism is present in the cooler southern waters:

Mollusca:	*Heterozona subviridus* Ired. & May, *Ischnoradsia evanida evanida* (Sow.), *Sypharochiton maugeanus* Ired., *Micrastrea aurea* Jonas, *Melarapha praetermissa* (May), *Dicathais textilosa* (Lam.), *Lepsiella vinosa* (Lam.), *Brachidontes rostratus* (Dunker), *Cellana solida* (Blainv.), *Notoacmea mayi* (May), *Patelloida victoriana* Singleton, *Patelloida latistrigata latistrigata* (Angas), *Siphonaria* (*Pachysiphonaria*) *funiculata* Reeve, *Siphonaria* (*Pachysiphonaria*) *tasmanica* Ten. Woods
Crustacea:	*Paragrapsus quadridentatus* (M. Edw.)
Echinodermata:	*Tosia australis* (Gray), *Pachycentrotus australiae* A. Aggasiz, *Ophioplocus bispinosus* H. L. Clark
Algae:	*Durvillea potatorum* Aresch., *Lithophyllum hyperellum* Fosli, *Xiphophora gladiata* (Lab.) Mont., *Lessonia corrugata* Lucas

The above, taken from the collecting lists of the present survey, includes only the commoner zoning indicators and a few of the common members of the cryptofauna. No attempt has been made to augment from literature records or collections in museums.

It is evident that among the truly intertidal species of the mid littoral, each of which must perforce be adapted to a widely fluctuating environment, many will be found ranging throughout warm and cool temperate areas, forming a substantial common "temperate" element, and among these may be listed species such as *Austrocochlea obtusa*, *Melanerita melanotragus*, *Bembicium nanum*, *Patelloida alticostata*, *Patellanax peroni*, and *Catophragmus polymerus*, and algae such as *Hormosira banksii*, *Pterocladia capillacea*, and *Cystophora paniculata*.

Among additional common elements, however, there are species which can generally be recognized as being better developed either at the warmer or cooler ends of the temperate region. The following may be mentioned as being favoured in warmer areas: *Patellanax chapmani* (T. Woods), *Notoacmea petterdi*, *Chthamalus antennatus*, *Balanus nigrescens*, *Galeolaria caespitosa*, *Pyura stolonifera*, *Patiriella calcar*, *P. gunnii*, and *Coscinasterias calamaria*, or algae such as *Ecklonia radiata* and *Corallina* spp.

Favoured towards cooler parts of the temperate are species such as *Chamaesipho columna*, *Ibla quadrivalvis*, *Ligia australiensis*, *Cyclograpsus audouinii*, *Subninella undulata*, *Mytilus planulatus*, *Modiolus pulex*, and *Poneroplax costata*, or algae such as *Codium pomoides*, *Chaetomorpha darwinii*, *Bryopsis gemellipara*, *Caulerpa brownii*, *Leathesia difformis*, *Xiphophora chondrophylla*, and *Adenocystis utricularis*.

Likenesses between the mid littoral zones of the warm and cool temperate provinces are, therefore, to be expected but even at this shore level differences in the populations are quite marked. There are, for instance, three species of limpets, two species of siphonarias, and the coralline alga *Lithophyllum hyperellum* which occur only in the cooler temperate areas of Tasmania and the south-east of the mainland.

The importance of the "sublittoral fringe" for making "geographic comparisons" has been commented upon by Chapman and Trevarthen (1953, p. 201), and this fact is well borne out along the east coast of Australia where three distinctly differing biotas occur:

(1) in the tropical seas north of latitude 25° S.,

(2) in the warmer temperate seas between 26° and 38° S.,

(3) on the shores of Tasmania between latitude 40° and 44° S.

The first of these is colonized by algae which are not specifically named but do *not* include *Ecklonia radiata* or *Phyllospora comosa* (Endean, Kenny, and Stephenson 1956). The actual sizes of these northern algae at the lowest shore levels are much smaller than those farther to the south, and are in some cases like a long algal turf. The corresponding level on the islands and reefs lying offshore in Queensland is usually characterized by coelenterate growths—alcyonarians, corals, and zoanthids, but these are only sporadic in their occurrence on the mainland intertidal zone (Endean, Stephenson, and Kenny 1956).

The second biota has been decribed by Dakin and the present authors (1948), and characteristically supports a thick growth of medium-sized brown algae in the infralittoral fringe, with *Phyllospora comosa* and *Ecklonia radiata* as dominants and an undergrowth of corallines including *Amphiroa anceps*, *Corallina officinalis*, *C. cuvieri*, *Jania natalensis*, lithothamnion, and *Arthrocardia* spp.

Each of these has its own range within the temperate areas and all are not to be found in every locality in the Peronian Province, but among them are the dominants which give character to the lowest intertidal area of this biogeographic province.

The third area in Tasmania, overlapping into Victoria to the north, is marked by the presence of the much larger giant fucoid, *Durvillea potatorum*, which, in sheer biomass per unit area of attachment, must greatly outweigh either of the two algal communities mentioned above. The only other significant species in the infralittoral fringe here are the encrusting lithothamnion, occurring between the large soup-plate sized holdfasts of the *Durvillea* and completely coating the rocks like pink paint, and *Xiphophora gladiata*.

Paralleling these distinctive infralittoral communities in the three geographic subdivisions are differing populations in the supralittoral fringe, though some of the high shore inhabitants range through more than one biogeographic area, as may be seen in the accompanying Table 2.

In each area, the combination of common high shore species differs, so that by noting those present it is possible to distinguish quite easily one geographic province from the next, and only in overlap areas is there any possibility of doubt. In the event of such doubt, the relative numbers and sizes of the different species will generally supply the answer as to whether "warmer" or "cooler" factors are dominant in the particular area under examination. It is significant that the changes in supralittoral fringe dominants occur in nearly the same latitudes as the changes in the infralittoral fringe species.

Womersley and Edmonds (1958) have produced percentage analyses of the total numbers of species of the common elements and of endemics in the various biogeographical provinces, and their figures show that a greater distinction exists between the eastern warm temperate (Peronian) and the cool temperate (Maugean), than between the section of the Flindersian Province examined by them and the present authors' Maugean. They also recognize a strong element common in the two latter biotas. On these grounds they would, therefore, relegate the Maugean biota to the status of a subprovince, and link it together with the biota of the cooler region of the western warm temperate (i.e. the area along the coast of South Australia), into one large cool temperate province.

TABLE 2

RANGES OF THE COMMON SPECIES ON THE UPPER SHORE ON EXPOSED COASTS OF EASTERN AUSTRALIA AND TASMANIA

Species	Tropical (Qld.)	Warm Temperate (N.S.W.)	Cool Temperate (Tas.)
Melarapha melanacme	————→		
M. unifasciata	←—	————	——→
M. praetermissa		←——	————→
*Nodilittorina pyramidalis**	————	————→	
Chthamalus withersi	———→		
C. antennatus	←	————	——→
Ligia australiensis		←——	————→

* *Nodilittorina tuberculata* of previous papers (see Endean, Kenny, and Stephenson 1956, p. 127).

It is considered, however, that their figures do not indicate the true state of affairs, for reasons which may be summarized as follows:

(1) A greater difference is to be expected between the warm and cool temperate biotas in the east in Australia than between those in the west, because of the additional presence, in the Peronian in the east, of a large Pacific element which finds no compensating factor in the west, owing to the west's geographical isolation and prevailing current systems.

The lack of a clearly defined change in populations, owing to the long overlap between the warm and cool temperate at the western end of the Maugean Province does not automatically lessen the reality of its existence. It merely makes the determination of the boundary more difficult.

(2) Generally, distributions of the animals and many of the zoning algae follow a like pattern, or have their ecological equivalents both to the east and west of the Maugean region. The only difference between the eastern and western warm temperate provinces, apart from the Pacific element mentioned above, is that the area of overlap in the west occupies a longer stretch of coastline, owing in large part to the direction in which the coast runs. The environmental conditions off much of

South Australia parallel those of southern New South Wales. If the biota of South Australia were to be included with that of Victoria and Tasmania in one cooler temperate zone, then the southern area of New South Wales, north perhaps to Narooma or even Ulladulla, would also have to be included, and this is clearly not as natural an arrangement as the one proposed in 1953.

(3) The present Maugean Province has its lower tidal zone completely dominated by the algae *Durvillea potatorum* (a giant fucoid), *Xiphophora gladiata*, *Lessonia corrugata*, and in less exposed areas by *Cystophora torulosa*, while offshore beds of the giant kelp *Macrocystis pyrifera* are found in suitable habitats, and there is no doubt that these species are rightly classed as cool temperate. Four of them are absent altogether on the coast of South Australia and the other (*Durvillea*) is present only in the most easterly section. Their place to the west is taken by species of *Cystophora*.

One reason given by Womersley and Edmonds for amalgamating their South Australia biota with that of the Maugean into a cool temperate area is the following:

> "Species of *Cystophora* reach 6 ft in length. It is difficult to say whether such genera should be classed as warm or cool temperate, but with *Durvillea* accepted as a cool temperate alga caution is needed in excluding other Fucales from "cool temperate" when their range coincides in part with that of *Durvillea*".

The greater length of the *Cystophora* spp. noted here is also paralleled in the more southerly regions of New South Wales by the alga, *Phyllospora comosa*, which grows to equally great lengths south of Ulladulla. Its range also overlaps that of *Durvillea* so that the occurrence of large-sized plants in the cooler (overlap) area of temperate biotas is not peculiar to South Australia. In warmer waters both these genera assume smaller growth habits.

(4) The published data on Tasmania available to Womersley and Edmonds may have proved misleading, for reasons outlined in Section III above, and also there is a lack of recent published data on the Western Australian section of the Flindersian Province.

(5) The analysis of algal distribution made by Womersley and Edmonds (1958, p. 252) on their own data gave an estimate of 17 per cent. of endemic species in the Maugean region. This 17 per cent. includes species such as *Durvillea potatorum*, *Lithophyllum hyperellum*, and *Cystophora torulosa*, all of which are extremely important from the point of view of biomass in the zoning pattern. Therefore, although this percentage may appear small, it is considered by the present authors to be sufficient to distinguish the Tasmanian zonation from that of the warm temperate areas. It is also highly likely that intensive algal collecting would raise the percentage to a considerably higher figure.

The Maugean biota is, upon mere inspection, quite distinct from that of other Australian provinces, and is characterized by the following cool temperate species which are common and significant in the zoning pattern:

Plants: Orange lichen, (mainly *Gasparinnia murorum*), *Lichina confinis*, *Codium pomoides*, *Splachnidium rugosum*,* *Cystophora torulosa*, *Xiphophora gladiata*, *Lessonia corrugata*, *Durvillea potatorum*, *Macrocystis angustifolia*, *M. pyrifera*, and *Lithophyllum hyperellum*.

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* Occurs only sporadically in New South Wales in winter.

Animals: *Melarapha praetermissa*, *Cellana solida*, *Lepsiella vinosa*, *Cominella lineolata*, *Notoacmea mayi*, *N. alta*, *Patelloida latistrigata latistrigata*, *P. victoriana*, *Siphonaria diemenensi*, *S. funiculata*, *S. tasmanica*, *Modiolus pulex*, *Brachidontes rostratus*.

The Maugean Province resembles the Namaqua region (the cool temperate) of South Africa in having a reduced total number of species and a small endemic element with many of its species ranging into adjacent warmer waters. On these grounds, Ekman (1935) challenged the validity of the Namaqua fauna as a distinct entity. Stephenson (1948, p. 244), however, considered that the picture in South Africa was obscured by a long-drawn-out overlapping of warm and cool temperate biotas which misled Ekman into denying the presence of a cool temperate region. According to Stephenson, however, the field evidence clearly showed its presence.

In Australia, the cool temperate elements among the common intertidal zoning organisms are more evident in Tasmania than they are in Victoria, but this fact has not been brought out clearly in the writings of previous workers on Tasmania, which provided the data upon which Womersley and Edmonds based their assumptions. It is considered that their recent survey of the South Australian intertidal has disclosed an area of long overlapping between adjacent warm and cool temperate provinces paralleled by that in South Africa, and that the arguments cited in favour of the cool temperate Namaqua fauna by Stephenson (1948, pp. 224–8), are equally cogent to the present case.

Womersley and Edmonds failed to recognize the overlap area as such since they dismissed from consideration the "warmer" section of the Flindersian Province, which is evident in the southern part of Western Australia, and extends across into South Australia.

Southward (1958, p. 149) suggests that the so-called "cool temperate" regions of the southern hemisphere should best be considered as "modified warm temperate". The authors have shown above, however, that the Maugean biota does differ considerably both from that of the Australian warm temperate region and from that described for the subantarctic Macquarie Island.*

The Maugean Province is, therefore, reaffirmed as being one of a cool temperate nature, the word "cool" being used deliberately, instead of "cold", since no part of the Australian land mass extends far enough south to penetrate really cold temperate or subantarctic waters. This province extends round the shores of Tasmania and along part of Victoria, with overlapping areas between warm and cool temperate regions existing in Victoria, southern New South Wales, South Australia, and in northern Tasmania.

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* Soon after the manuscript of this paper was submitted for publication, one of the authors (I. B.) was given the opportunity of visiting Macquarie Island, and is thus able personally to verify this difference.

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Mr. A. Hewer collected specimens, and photographed places inaccessible by ordinary transport in the south-west. Mr. D. Kurth took photographs along a stretch of the west coast inaccessible to transport. Dr. A. B. Cribb gave us specimens and photographs, and Mr. R. C. Kershaw collected specimens for us on the north coast.

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Explanation of Plates 1–7

Plate 1

Fig. 1.—Platform exposed to maximum seas and westerly gales. A well-developed band of *Lithophyllum hyperellum* is seen in the foreground above the *Durvillea* at Cape Sorell.

Fig. 2.—Typical occurrence of *Phyllospora comosa* in deep sheltered pool in the infralittoral fringe. A few plants of *Macrocystis angustifolia* were growing among it. (Hunter Island.)

Plate 2

Fig. 1.—A well-developed coralline weed mat above the *Durvillea* holdfasts at Sandy Cape on the west coast.

Fig. 2.—Very narrow band of corallines above the holdfasts of the *Durvillea* at Tasman Island. The chiton *Poneroplax costata* and the limpet *Patellanax peroni* are common at this level.

Plate 3

Fig. 1.—Close-up of the infralittoral fringe at Bicheno. *Durvillea potatorum* with *Xiphophora gladiata* in the foreground just above it.

Fig. 2.—Dense growth of *Lithophyllum hyperellum* at Sandy Cape. The limpet is *Patellanax peroni*, and the chiton *Poneroplax costata*.

Plate 4

Close-up of vertical zonation on reef at Pirates Bay. Dense mat of *Brachidontes* on top (horizontal) surface, with barnacle *Catophragmus* attached, and below this sparse corallines with chiton, *Poneroplax*, then *Pyura* band with *Poneroplax* and scattered *Mytilus* among it.

Plate 5

Fig. 1.—Dense mat of *Brachidontes rostratus* on sheltered reef, Pirates Bay, Tasman Peninsula.

Fig. 2.—The barnacle *Catophragmus polymerus* above narrow coralline belt on granite platform, Cape Forestier.

Plate 6

Fig. 1.—The limpet *Notoacmea mayi* with scattered *Chamaesipho* on vertical rock face, Cape Sorell.

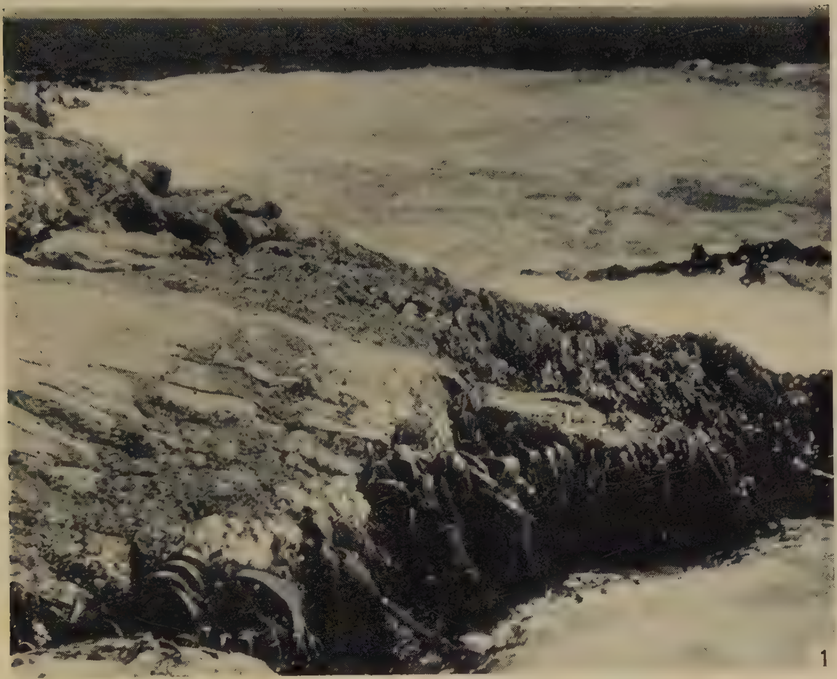
Fig. 2.—Juveniles of *Notoacmea mayi* before migration to higher levels, outer platform, Eaglehawk Neck. The barnacle is *Catophragmus polymerus*.

Plate 7

Fig. 1.—Dark clusters of the small mussel *Modiolus pulex* among the barnacle *Chamaesipho* at Three Hummocks Island. The dark weed in the pool is *Ulva lactuca*. There was no sand among these mussels.

Fig. 2.—*Modiolus pulex* can tolerate quantities of sand among individuals in a clump, as may be seen in the dense growths attached to sand-embedded rocks at Green Point, Marrawah.

INTERTIDAL ZONATION OF TASMANIAN SHORES



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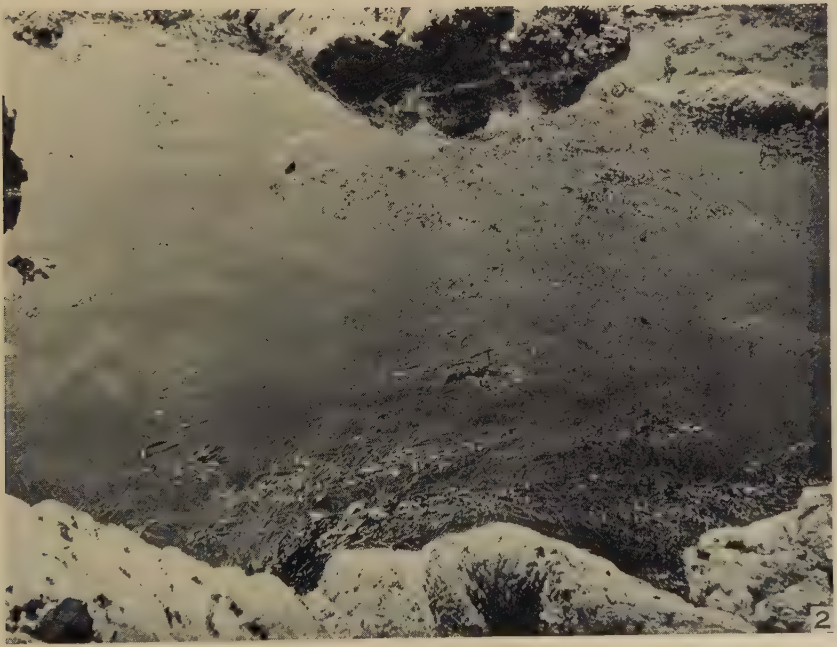

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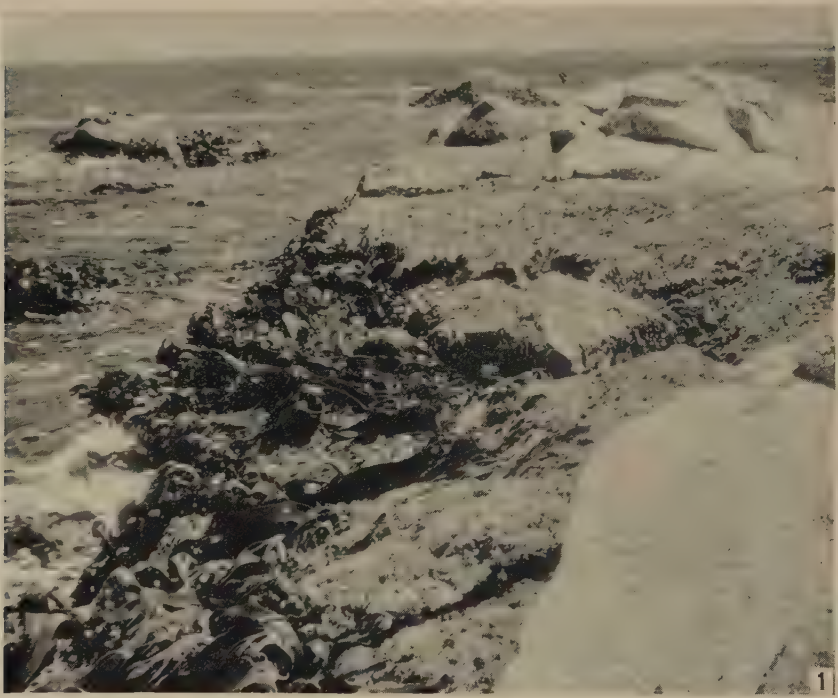
INTERTIDAL ZONATION OF TASMANIAN SHORES



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INTERTIDAL ZONATION OF TASMANIAN SHORES

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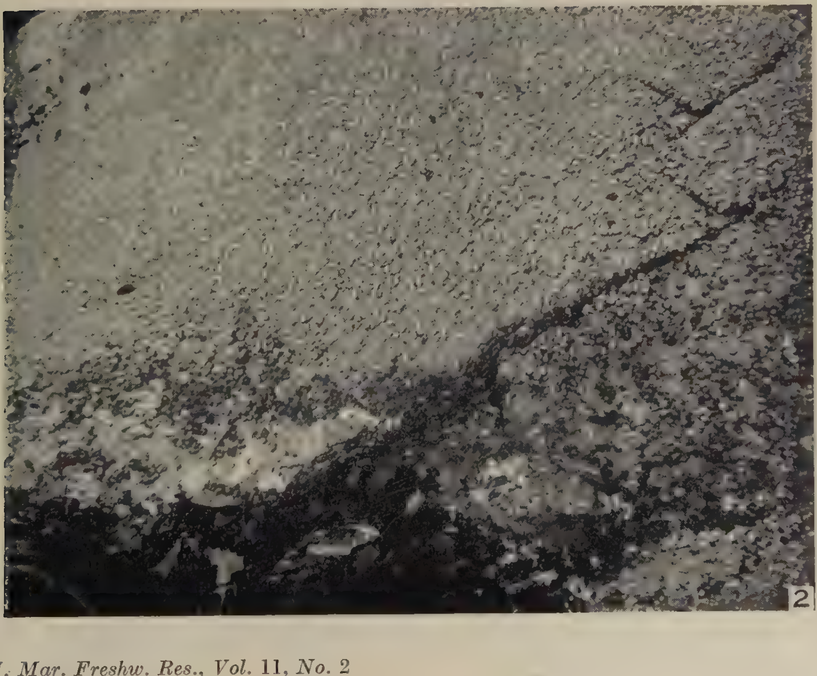

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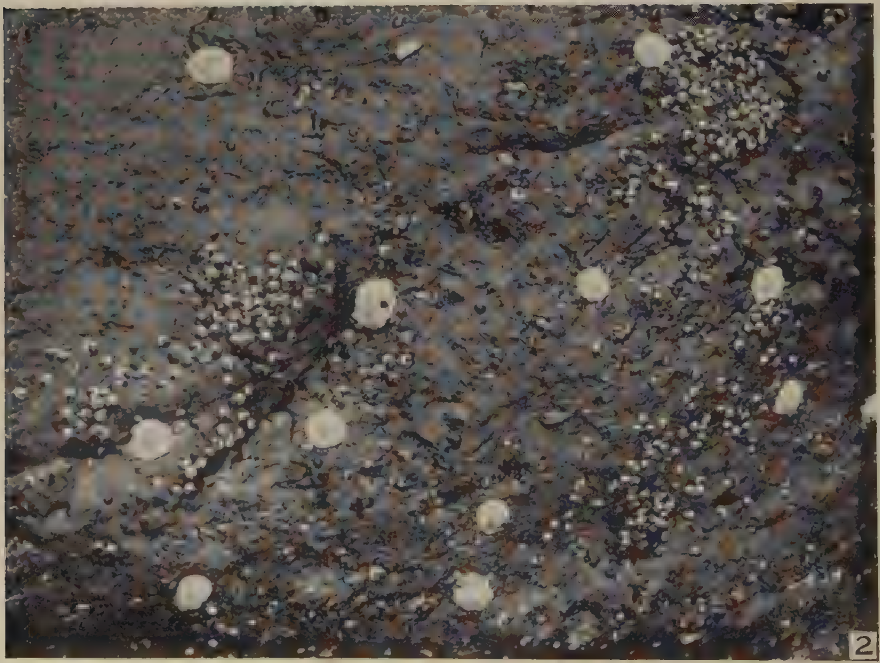

INTERTIDAL ZONATION OF TASMANIAN SHORES

1

2

Appendix I

DEGREES OF EXPOSURE

Maximal exposure is the term used to describe areas where strong, regular surf pounds on the shore at all times except on rare occasions of exceptional calms and strong offshore winds. The waves are large enough and strong enough to make working near low water mark dangerous or impossible; e.g. west coast of Tasmania at Cape Sorell.

Submaximal exposure is encountered where offshore stacks, low rocky reefs, kelp beds, or a projecting small promontory mitigate to a slight degree the force of a surf as described for "maximal exposure". The area of submaximal exposure is constantly subjected to waves of white, foamy water which have "broken" on the obstructions mentioned above. With care it is possible to work in the area, and not be knocked down or washed off the rocks by waves surging over them; e.g. south coast, Remarkable Cave area.

Moderate exposure is experienced when surf without much force constantly washes over the rocks. In storms from the right direction such an area might move up into the submaximal category, but rarely into the maximal one; e.g. Pirates Bay rocky reef with mussel beds.

Sheltered open coast experiences small waves without great force, and choppy seas and surge rather than surf; e.g. north coast, Waterhouse Point, Wivenhoe.

A FRESHWATER POND IN NEW ZEALAND

By Jean A. Byars*

[*Manuscript received December* 11, 1959]

Summary

A year's survey of the fauna and flora present in a freshwater pond provides the first work of its kind recorded in New Zealand.

Attention was given to the effect of the recorded chemical and physical factors on the fluctuations in number of the zooplankton. A comparison of the local phytoplankton and zooplankton with those from similar studies in North America, Europe, and Asia shows the cosmopolitan nature of the inhabitants of freshwater.

I. Introduction

The main objective of this survey was to obtain some general data on the life present in a freshwater pond. The seasonal fluctuations in number of the various zooplanktonts were given special consideration and an attempt was made to correlate these fluctuations with recorded chemical and physical factors.

In New Zealand previous publications of limnological work have been concerned with large bodies of water only—Lake Taupo (Armstrong 1935), Lake Sarah (Flint 1938), Wellington Reservoirs (Stevenson 1951), Lake Hayes (Jolly 1952), and North Island Coastal Dune Lakes (Cunningham *et al.* 1953). As yet there has been no survey of the plankton population of a pond throughout a year.

Two main reasons made Saddle Hill Pond a suitable one for study, namely its isolation and its recent origin. Firstly, the pond may be considered to be natural as it is lying on farmland about $\frac{3}{4}$ mile from the road and farmhouse and so it is free from human contamination. Secondly, it was formed in 1929 when, after a particularly heavy rainfall, a landslip blocked a narrow gully. Because of its recent formation it provides an opportunity for a study in pond evolution.

Owing to the limits imposed by time, the detailed study was restricted to the zooplankton while some information as to the nature of the fauna of the mud and weeds, the free-swimming animals, and the surface dwellers was gained by occasional sampling.

II. Geological and Morphological Features

The top of Saddle Hill is composed of basaltic rocks; the lower slopes consist of glauconitic Abbotsford mudstone and overlie quartz sandstone coal measures, the latter being in contact with the basement rock, Otago schist. The Abbotsford mudstone is very prone to slide and it was a landslip which caused the formation of the pond in a narrow gully.

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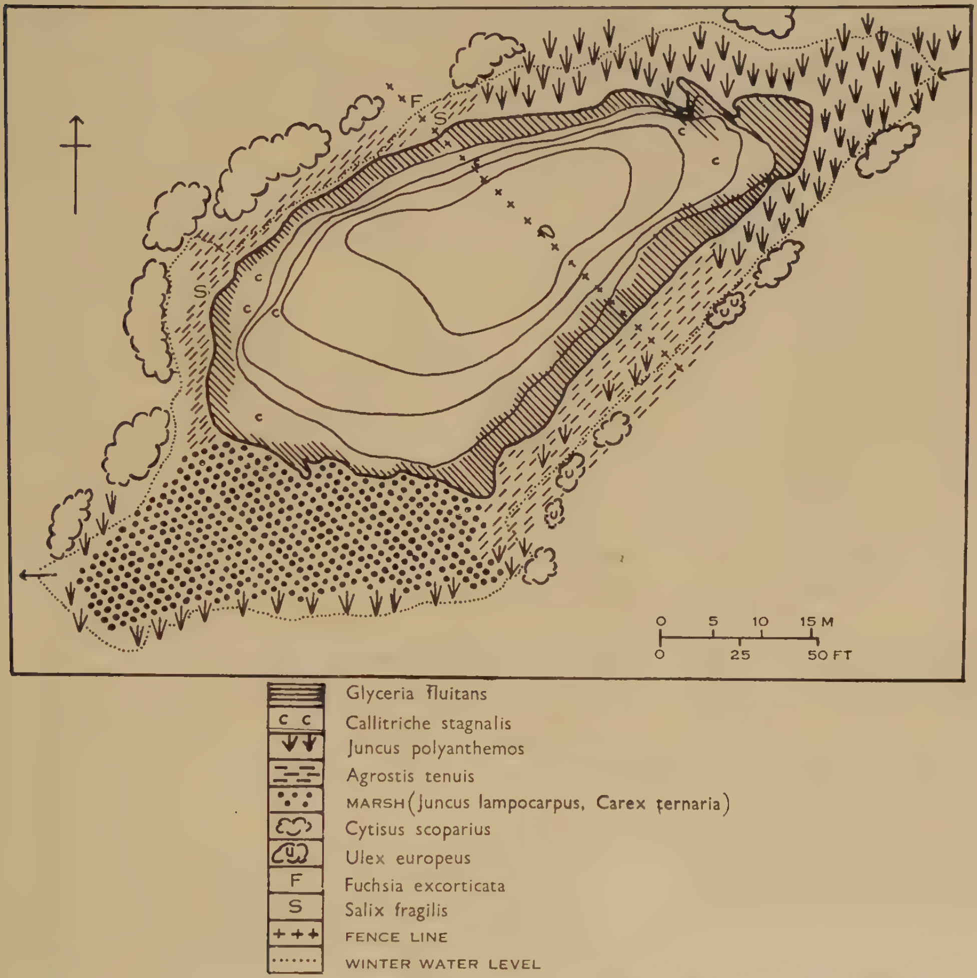
The pond lies 400 ft above sea-level on the western side of Saddle Hill, 8 miles south-west from Dunedin. The east side is bordered by a slope of mudstone, while the west side is a much steeper schist spur. The bottom of the pond is composed of a layer of grey-brown mud and schist particles of various sizes. The average organic content of the mud, found by heating dehydrated samples to 800°C for half an hour, was approximately 10 per cent.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Glyceria fluitans
c c Callitriche stagnalis
Juncus polyanthemos
Agrostis tenuis
MARSH (Juncus lampocarpus, Carex ternaria)
Cytisus scoparius
U Ulex europeus
F Fuchsia excorticata
S Salix fragilis
+ + + FENCE LINE
WINTER WATER LEVEL

Fig. 1.—Map of Saddle Hill Pond showing the summer and winter water levels and the vegetational features.

Saddle Hill Pond is a seepage pond, consequently the water level shows marked correspondence with the amount of rainfall. Two shore-line surveys were made by the method described by Welch (1948, p. 21), the first in February when the water was at a low level and the second in August when the shore-line was considerably extended. The length varied from 63 to 97 m and the width from 34 to 47 m at midsummer and midwinter respectively. Soundings were taken on both occasions and it was found that the depth in the centre increased from 2·2 to 3·5 m. The surface area varied from 1270 to 2936 sq. m.

For the greater part of the year the pond is completely isolated as there are no streams entering or leaving it. Occasionally in the winter, after heavy rainfalls, a small inflowing stream was formed in the gully at the north-east end. There was no direct outflow, but at the south-west margin the water escaped by seepage and appeared as a temporary outflow about 15 ft from the end of the pond and drained down the lower gully.

III. VEGETATION

A striking feature of Saddle Hill Pond is the lack of a variety of rooted aquatic plants growing in the littoral region, owing probably to the youthful state of the pond. On the shore, clumps of *Juncus polyanthemos* are numerous, especially around the north end as far as the fence line across the centre of the pond, while scattered plants also occur at the south end. In winter and early spring, water covers the roots of most of these plants, which then would represent the zone of rooted emergent vegetation. At the south end is a marsh formation of *Juncus lampocarpus* and *Carex ternaria*, which is completely submerged during the wet season.

Below the line of *Juncus polyanthemos*, *Glyceria fluitans* (an exotic grass) extends from the banks into the pond to a depth of approximately 1 m, and forms a zone of partly submerged vegetation, equivalent perhaps to the *Nymphaea* zone of other ponds. The only completely submerged rooted aquatic is *Callitriche stagnalis*, which occurs sparsely at depths of ½–1½ m. It does not form a continuous ring within the pond, probably because it has only recently made its appearance.

A floating pteridophyte, fairly common throughout the year, is *Azolla rubra*. Algae present included filamentous and blue-green species and diatoms, all of which are discussed under the phytoplankton.

On the western side at the water's edge are two medium-sized willow trees, *Salix fragilis*, one at the fence line and the other at the south-west end. A native tree, *Fuchsia excorticata*, also stands at the fence about 3 ft behind the willow.

A grass, *Agrostis tenuis*, broom, *Cytisus scoparius*, and some gorse, *Ulex europeus*, form the main vegetative covering farther up the banks, the broom being especially prevalent on the schist spur.

A notable characteristic is the prevalence of exotic plants which are in greater abundance than the native species. The vegetational features are recorded in Figure 1.

IV. METHODS

(a) *Physical*

(i) *Temperature*

Air and water temperatures were taken using a maximum–minimum thermometer. The air temperatures were recorded 3 ft above the ground, in the shade of the willow which is growing at the fence line.

The water temperatures were recorded at half-metre intervals from the surface to the bottom. All measurements were made at the centre of the pond, and Figure 2 shows the relationship between the water and air temperatures:

Maximum air temperature: 26·6°C on February 19, 1954.

Minimum air temperature: 4·4°C on July 17, 1954.

Maximum water temperature: 20·0°C on December 29, 1953.

Minimum water temperature: 2·8°C on August 1, 1954 (ice on part of pond).

There is no seasonal stratification of the water into an epilimnion and a hypolimnion, but the temperature of the whole volume of water follows the seasonal atmospheric changes in temperature; however, during the warmer months a slight stratification of the water was noticed on several occasions—viz. in February, September, October, and November. For example the variation on February 12, 1954, was from 20°C at the surface to 16·1°C at 2 m; and on October 7, 1954, the temperature was 15·5°C at the surface to 11·7°C at 2½ m. The stratification was readily upset by winds and did not remain for more than one or two days at a time—the clear temperature gradient recorded on October 7, 1954, had completely disappeared by October 9 owing to a blustering south-west wind and the water at all levels was 12·2°C.

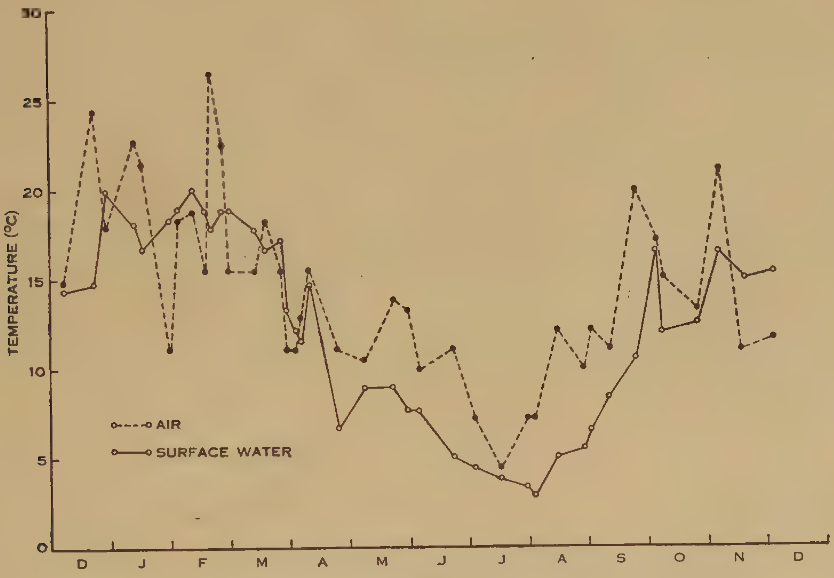

Fig. 2.—Air and surface water temperatures, December 1953 to December 1954.

When ice was formed over a large area of the pond, an inverted temperature gradient was recorded. On August 1, 1954, the surface temperature at the centre was 1·1°C and at 2½ m it was 3·9°C.

(ii) *Light Penetration*

The colour of the water is yellow-brown and the pond appears to have a moderately low transparency.

A standard Secchi disk, as described by Welsh (1948, p. 159), was used to determine the limit of visibility in the deepest part. The readings varied from 1 to $2\frac{1}{2}$ m; however, no significance can be attached to the results when they are correlated with the weather conditions prevailing at each visit.

Surface Illumination.—In winter only the eastern half of the pond was directly illuminated by the sun's rays, even at midday. During June and July the western side was shaded by the steep bank.

(iii) *Rainfall*

A rainfall gauge with a standard diameter of 5 in. was placed at the north end, and readings were taken at each fortnightly visit. A comparison of these readings with those taken at the Taieri Meteorological Station, 3 miles away, shows that the pond has a slightly higher rainfall owing to its altitude. When the Taieri records of the annual total rainfall for 1954 are compared with those for 1947–53 it is found that for the year December 8, 1953, to December 6, 1954, the rainfall was slightly heavier than for the previous few years.

There is a marked correlation between the amount of rainfall and the water level. A rod marked in centimetres was placed at the west side of the pond to record the fluctuations in water level. The water fell to the 20-cm mark (7·8 in.) during February and rose after heavy rainfalls in June, July and August to 150 cm (59·0 in.). The extent of the alteration in level of the pond was therefore 1·3 m or $4\frac{1}{4}$ ft.

(iv) *Wind*

The prevailing winds are north-east, south-west, and west.

(*b*) *Chemical*

(i) *Oxygen Estimation*

Water was collected in Hale's water sampler, described by Welch (1948, p. 202, Fig. 60), and the method of estimation was the alkaline–azide modification of the Winkler method, as employed by the Department of Scientific and Industrial Research. Each fortnight two samples were taken from the centre of the pond, one at $\frac{1}{4}$ m and the other at 2 m. There was little difference in the oxygen content of the two samples; any variation showed that the upper sample contained slightly more oxygen but there was on the average a difference of no more than 0·2 ml per litre.

The results are recorded in Figure 3 and it can be seen that there was never a deficiency of oxygen. Supersaturation occurred in the warmer months, from late December 1953 until mid February 1954. The rise in oxygen content at this time was probably due to the activity of the plant life. Similarly, the noticeable rise during April must have been due, in part at least, to the great abundance of an alga, *Gloeocystis* sp.

Rawson's nomogram (Welch 1948, p. 366), was used to find the percentage saturation of the oxygen. The highest degree of saturation was 117 per cent. on January 13, 1954, and the lowest was 65 per cent. on November 11, 1954.

(ii) *Free Carbon Dioxide*

Hale's apparatus was used to collect water at $\frac{1}{4}$ m depth for the estimation of free carbon dioxide by the method described in a paper by Mortimer and Mackereth (1949). There was a trend towards a greater amount of dissolved carbon dioxide during the winter months.

(iii) *pH Determination*

Once a fortnight the pH of the water was determined at the pond with B.D.H. Universal indicator and a standard colour chart. An additional check was made with a pH meter. There was a slight variation during the year, the pH ranging from 6·3 on January 13, 1954, to 7·0 recorded on March 13 and June 5, 1954. The trend towards acidity increased during the summer.

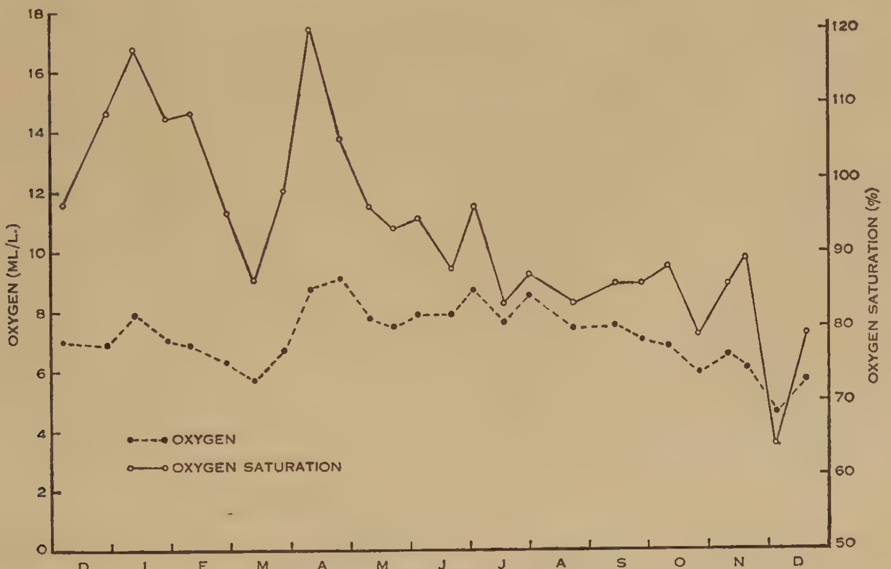

Fig. 3.—Oxygen content and saturation of the water, December 1953 to December 1954.

(iv) *Chemical Analysis*

The results of three water analyses, performed by the Department of Scientific and Industrial Research, are shown in Table 1. The samples were taken in a 3-l. bottle from the centre of the pond about 6 in. below the surface, on three occasions—April 8, July 7, and November 11, 1954.

(*c*) *Biological*

(i) *Plankton*

The method of plankton sampling best suited to this small body of water was collection by tow-net. Two nets, each with a diameter of 15·0 cm and a length of 40·5 cm, were used; one of 4XX bolting silk for zooplankton and the other of 9XX bolting silk for the phytoplankton. At the end of each net was a small glass funnel which led into a piece of rubber tubing closed by a screw clip.

Once a fortnight a double haul (to and fro) was made at each of three positions—at the north end, the fence line, and by the willow at the south end. The collections were run into preserving bottles and 4 per cent. formalin was added.

It is considered that a comparison may legitimately be made of the results of successive samplings if the speed and distance of the hauls are consistent.

Enumeration.—For identification and enumeration the samples were pipetted in 3-ml lots into a rectangular Perspex counting cell, 7 cm long by 4 cm wide, and divided longitudinally into three compartments. A binocular microscope with a ×12·5 eyepiece and a 2½-in. objective gave a sufficient magnification for the ready identification of the larger plankton constituents, i.e. the microcrustacea, the rotifers, and most of the algae. The whole of each plankton sample taken at the respective stations was examined and the individuals were counted.

Table 1

CHEMICAL ANALYSIS OF THE POND WATER

Determination	8.iv.54	7.vii.54	11.xi.54
Smell	—	—	—
pH	6·8	6·5	6·6
Chlorides (p.p.m. Cl)	43·5	41·0	43·0
Nitrate N (p.p.m.)	—	—	—
Nitrite N (p.p.m.)	—	—	—
Ammoniacal N (p.p.m.)	—	0·035	—
Albuminoid N (p.p.m.)	0·780	0·446	0·346
Oxygen absorbed in 4 hr at 80°F (p.p.m.)	3·30	3·92	3·55
Total solids (p.p.m.)	145	143	130
Iron (p.p.m. Fe)	0·50	—	1·50
Total Hardness (p.p.m.)	38·0	33·0	33·0
Silica (p.p.m.)	3·0	6·0	trace
Phosphate	faint trace	trace	trace

Whenever possible, specimens were sent to authorities for identification and in the case of other groups, identification was carried to family, genus, or species level, whichever the available literature would allow. Complete floral and faunal lists are given in Appendices I and II.

(ii) *Additional Fauna*

(1) To gain some knowledge of the fauna living on and in the sediments, two series of mud samples were taken with a Petersen Dredge of approximately 2 l. capacity. On April 7 and October 7, 1954, nine samples were removed from various points around the margin and towards the centre of the pond and passed through a three-layered sieve.

There were few species present, owing perhaps to the recent origin of the pond. On each occasion the fauna was composed of large numbers of oligochaetes, *Potamopyrgus* spp., *Corniocyclas* sp., and *Herpetocypris pascheri*, and also a few chironomid larvae, *Simocephalus* ephippia, and dytiscid larvae.

At the laboratory the organic content of the mud from each sampling point was estimated by incineration. In autumn the organic content varied from 5 to 10 per cent. and in spring from 6 to 12 per cent. The increase of the organic constituent in spring is probably due to the amount of animal and vegetable material which had undergone decomposition during the winter months.

(2) Sampling of the marginal vegetation of *Glyceria fluitans* was done in October. Six samples of weed were removed and placed in glass aquaria under tap water. After one week the animals floated to the surface and were easily removed.

Large numbers of *Potamopyrgus* species at all stages of development were present and also small numbers of the following, *Cypridopsis* sp., *Herpetocypris pascheri*, *Glossiphonia* sp., oligochaetes, *Planaria* sp., *Hydra viridissima*.

A few insects were taken from a trap placed at the water's edge. Some were emergent and some were surface dwellers, and they are listed here:

Odonata:	*Austrolestes colensonis*
	Xanthocnemis zelandica
	Aeschna brevistyla
Hemiptera:	*Microvelia macgregori*
Diptera:	*Hercostomus argentifacies*
	Hydrellia enderbyi

(iii) *Phytoplankton*

Phytoplankton included species of the filamentous algae *Spirogyra*, *Zygnema*, *Mougeotia*, *Sirogonium*, *Oedogonium*, and *Bulbochaete*. Also of frequent appearance were *Cosmarium*, *Closterium*, and *Oscillatoria* spp. A few individual species made noticeable seasonal increases, amongst which was *Gloeocystis* sp. in the autumn, and in the spring diatoms became very numerous; especially so were *Asterionella* sp., *Navicula* spp., *Gomphonema* spp., and *Synedra* spp.

To add to the qualitative knowledge of the fauna and flora of the water, glass slides were suspended at intervals of ½ m in the centre of the pond and left for a period of 4–5 weeks when they were removed and examined. The glass slide method is recommended by Welch (1948, p. 262) and has been used by Young (1945) in investigations in North America.

(iv) *Standing Crop*

Riley (1940) states that a rough estimation of the productivity of a body of water may be made by measuring the standing crop. For the present investigations, a 3-l. sample was filtered and then centrifuged at a speed of 2000 r.p.m. for ½ hour. The supernatant water was removed and the remainder recentrifuged in smaller bottles for 15 min at 2500 r.p.m. The subsequent centrifugate was dried in an oven for 24 hours at 100°C. After cooling in a desiccator, the material was weighed in a porcelain crucible and placed in an electric furnace where it was incinerated at 800°C for 1 hour. The amounts of the standing crop were: June 2, 1954, 4·0 mg/l.; June 22, 1954, 4·6 mg/l.: August 19, 1954, 2·88 mg/l.

V. Biological Results

(a) *Occurrence of the Planktonic Species*

In order to discover something of the seasonal features of the life cycle of *Boeckella triarticulata*, differentiation was made between males, females, young, and females carrying eggs when counting the plankton samples. No such distinction was made with the other copepods.

At no time were male Cladocera of any species found. Other animals which commonly occurred in the samples were: ostracods, rotifers, oligochaetes, *Difflugia* sp., and various Hemiptera and Coleoptera. From the results of each count made of samples taken at fortnightly intervals throughout the year Figure 4 has been constructed to elucidate the seasonal occurrence of the more abundant of the zooplankters.

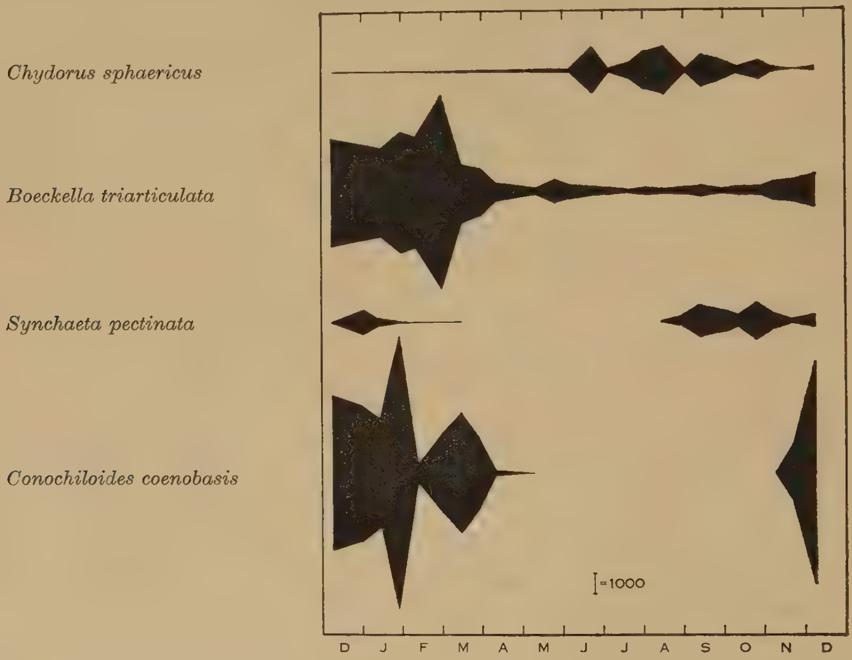

Fig. 4.—Seasonal abundance of the major zooplanktonts, December 1953 to December 1954.

In Table 2 the occurrence of each species is shown as it appeared in the fortnightly collections. The different species are divided into five groups on the basis of their distribution in time. It is realized, however, that one year's sampling gives only an indication of the seasonal occurrence of a species.

(b) *Seasonal Fluctuations of the Major Groups*

The numbers of Cladocera, Copepoda, Ostracoda, and Rotifera collected each fortnight at the three stations, when compared with the total zooplankton population, showed that for a large part of the year the Copepoda formed the main group. From December 1953 until the beginning of April, *Boeckella triarticulata* and *Conochiloides* *coenobasis* were the most abundant species (Fig. 4). A peak on January 30 was largely composed of *B. triarticulata* and *C. coenobasis* but there was also a peak of *Simocephalus vetulus* var. *elizabethae* on that date.

From the beginning of April until the beginning of June, the population was almost entirely composed of Copepoda. During this period the Rotifera had completely disappeared and there were few Cladocera and still fewer Ostracoda.

By June 22, a large number of *Chydorus sphaericus* had appeared, and this species was the dominant member of the zooplankton until August. A winter peak on June 22 was composed mainly of *Chydorus sphaericus*, but maxima of *Cyclops fimbriatus*, *C. viridis*, and *Cypridopsis* sp. occurred simultaneously and also contributed.

By August 29, the Cladocera were showing a tendency to decline, but fluctuated throughout September and October. Meanwhile, the Rotifera, represented mainly by *Synchaeta pectinata*, had dramatically reappeared to swell the population numbers.

During October and November, the Cladocera declined in number but the population was augmented by the increase of the Copepoda (mainly *Boeckella triarticulata*), and the rotifer, *Conochiloides coenobasis*.

Throughout the year the ostracods played a minor part in the total count.

A comparison of the numbers of the species present indicated that the population during December of 1953 and in December 1954 had a similar relative composition.

Predatory animals such as the backswimmers and *Chaetogaster* sp. doubtless would affect the numbers of the various species. No quantitative measurements were made to estimate this factor but it is recognized as a feature of considerable importance in controlling the population numbers.

VI. Discussion

The phenomenon of seasonal periodicity is exhibited by the plankton population in Saddle Hill Pond, but information as to the nature of the spatial as well as the temporal distribution of the animals is required in order to form a complete picture of the habits of the zooplankton constituents. The diurnal vertical migrations of zooplankton organisms are a recognized feature of aquatic life and the spatial distribution of the organisms is affected by the same factors which regulate the seasonal periodicities, viz. light, temperature, chemical conditions, and food materials. It is known that light is the main factor which controls these movements (Ruttner 1953, p. 131). Unfortunately it was not possible to take samples at night on the occasion of each field trip during this investigation, and so the previously described technique, which provided adequate seasonal figures, was adopted.

Consideration will now be given to the extent of the influence of the potential limiting factors, previously described, upon the seasonal periodicities of the zooplankton population. Under normal conditions oxygen becomes a limiting factor at concentrations of 1–2 mg/l. (Ruttner 1953, p. 133). At Saddle Hill Pond the lowest recorded value of oxygen was 4·55 ml/l., which is equivalent to 6·5 mg/l., representing a degree of saturation of 65 per cent. Wind action prevented any marked degree of stratification and all parts of the pond had a plentiful supply of oxygen at all times. It is therefore assumed that oxygen played no critical part as a limiting factor.

TABLE 2

SPECIES FOUND DURING FORTNIGHTLY VISITS, DECEMBER 1953 TO DECEMBER 1954

A, abundant (over 100); C, common (over 40); f, few (over 10); r, rare (under 10); —, absent

Species	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Group I. Species of Constant Occurrence													
Difflugia corona	CC	ff	rr	rr	rf	ff	fC	fff	ff	rf	rf	Cf	r
Group II. Species not Constantly Present but Occurring without Pronounced Reference to Season													
Ilyocryptus sordidus	r—	—r	——	——	——	——	——	———	——	——	rf	——	—
Group III. Forms with a Tendency toward one or two Periods of Abundance but not Limited to these Seasons													
Hydra viridissima	ff	fr	——	—r	rf	fr	fA	frA	AA	C—	r—	fr	r
Chaetogaster sp.	rr	—r	——	r—	rr	rr	fC	rrC	AC	fr	r—	rr	r
Alona eucostata	——	——	—r	——	——	——	rr	r—r	rr	rr	——	——	r
Boeckella triarticulata	AA	AA	AA	AA	AA	AA	AA	CfC	CC	CC	CC	CA	A
Chydorus sphaericus	rr	—r	rr	rr	ff	fC	CA	AAA	AA	AA	AA	Af	C
Simocephalus vetulus var. *elizabethae*	Af	fA	ff	Cf	rf	rr	fC	frA	Ar	rf	rr	rC	C
Cyclops viridis	fr	rr	r—	rr	rf	rr	fA	CCA	AC	CC	Cf	ff	f
Cypridopsis sp.	—r	rr	—r	rr	—r	——	—C	frC	Ar	rf	rr	rr	r
Anisops assimilis	ff	fr	rr	r—	—r	——	—r	———	——	r—	r—	—f	f

TABLE 2 (*Continued*)

Species	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
					Group IV. Forms with Sharply Limited Seasonal Distribution								
Synchaeta pectinata	CA	Af	—C	C—	— —	— —	— —	— — —	fA	AA	AA	AA	A
**Lecane inopinta*	— —	— —	— —	— —	— —	— —	— —	— — —	— —	Af	—r	— —	—
Keratella quadrata var. *edmondsi*	— —	— —	—r	— —	— —	— —	— —	— — —	— —	—r	rf	fr	r
Testudinella patina	— —	— —	— —	— —	— —	— —	— —	— — —	—r	fr	rr	rr	—
Filinia longiseta	r—	— —	— —	— —	— —	— —	— —	— — —	— —	—r	ff	f—	—
**Conochiloides coenobasis*	AA	AA	AA	AA	AC	— —	— —	— — —	— —	— —	— —	rA	A
Camptocercus australis	— —	— —	— —	— —	— —	—r	rf	rrr	rr	rr	r—	— —	—
Cyclops fimbriatus	— —	— —	— —	— —	— —	— —	rC	frr	rr	r—	— —	— —	—
Herpetocypris pascheri	— —	— —	— —	— —	rr	rr	rr	frr	fr	rr	— —	— —	—
					Group V. Transient Planktonts								
Daphnia carinata var. *thomsoni*	— —	— —	rr	rr	— —	— —	— —	— — —	— —	— —	— —	— —	—

* Not previously recorded in New Zealand.

Carbon dioxide was present on all occasions and is not considered to be of significance as a limiting factor.

Of the dissolved salts, nitrogen and phosphorus are of major importance for they, together with carbon and hydrogen, are the main constituents of protoplasm. Small amounts of each were present throughout the year, but it is not possible to assess their values as limiting factors without experiment. There does not seem to be a correlation between the various forms of nitrogen and the plankton growth.

The chemical analyses of the water showed that there was very little variation in conditions throughout the year, apart from the drop in silica content after the diatom peak in spring. No direct relationships can be deduced between the chemical conditions and the plankton population at any specific time.

Table 3

CLASSIFICATION OF PLANKTON SPECIES ACCORDING TO FINDENEGG (1943)

	Weak-Light Forms	Strong-Light Forms
Cold-water forms	Winter plankton, e.g.: *Chydorus sphaericus* *Cyclops fimbriatus* *C. viridis* *Camptocercus australis* *Alona eucostata* *Chaetogaster* sp.	Spring plankton, e.g.: Rotifera *Synchaeta pectinata* *Lecane inopinta* *Testitudinella patina* *Filinia longiseta* *Keratella quadrata* var. *edmondsi* *Cypridopsis* sp.
Warm-water forms	Fall plankton, e.g.: *Boeckella triarticulata* *Daphnia carinata* var. *thomsoni*	Summer plankton, e.g.: *Simocephalus vetulus* var. *elizabethae* *Boeckella triarticulata* *Anisops assimilis* *Conochiloides coenobasis*

Light becomes an important limiting factor at greater or lesser depths, depending on the degree of penetration allowed by the colour of the water and the amount of suspended material. The Secchi disk readings provide the information that throughout the year there was no marked change in the amount of light penetration.

Of the possible limiting factors, temperature would appear to exhibit the greatest effect on the periodicity of the zooplankton, especially the Rotifera which have limited temperature ranges.

In temperate latitudes the duration of illumination, as well as the temperature, plays an important part in governing the appearance of planktonts. Findenegg (1943), has proposed a classification for the occurrence of plankton according to their light and temperature requirements. This is applied to the fauna under consideration in Table 3.

From the foregoing observations it appears that temperature is the most important single factor in controlling the plankton population. Temperature and, to some degree, light played a great part in inducing seasonal fluctuations in numbers and in controlling the appearance and disappearance of various species as the yearly cycle progressed.

The seasonal changes in abundance of certain of the zooplanktonts in Saddle Hill Pond show some points of similarity to and some of contrast with those which take place in ponds in the Northern Hemisphere.

A point to be remembered is that the local winter is not so rigorous as that experienced in parts of Britain, Europe, and North America. In those regions, ponds are often covered with ice for periods up to several weeks, whereas in the pond under consideration, when ice was formed it was very thin and had always melted by midday.

Smyly (1952) observes that in Wise Een Tarn, *Chydorus sphaericus* showed a considerable spring peak (at a temperature of 6–8°C), but was scarce throughout the remainder of the year. In Saddle Hill Pond, winter and early spring population increases occurred (the temperature was 5°C), and these were followed by a decline in numbers, a condition which parallels that in Britain. In North Europe, Lilljeborg (1900) has found this species throughout the year, even beneath the ice in winter. Ward (1940), from her study of ponds in Cincinnati, has recorded this species as being absent in winter from shallow pools, but present throughout the year in deeper ponds. No comparative numbers are given by Lilljeborg or Ward, so that the relative seasonal abundance in these regions is not known. *Chydorus sphaericus* has also been reported from China (Hsiao 1949; Mashiko 1951*a*) and from Japan (Mizuno 1953). Mizuno recorded the species in a pond in the northern part of Osaka Prefecture, when it occurred for a limited period from August until December, i.e. late summer to winter. A peak was observed during September, a contrast with the winter and spring peaks of New Zealand and Britain. In Central China, Mashiko (1951*b*), found *C. sphaericus* during most months of the year. An early spring peak occurred (February) and the species was common until the end of March. Few specimens were reported throughout the remainder of the year, and it appears that the periodicity exhibited by the species in Central China is comparable to that observed here.

Cyclops viridis is recorded here as being present all through the year, with an increase occurring in winter. Similar behaviour of members of this species has been found in Britain (Smyly 1952) and in North America by Ward (1940).

In Britain, *Diaptomus gracilis* was present throughout the year in Wise Een Tarn (Smyly 1952). When the annual fluctuations of this copepod are compared with those of its ecological equivalent in the Southern Hemisphere, *Boeckella triarticulata*, it is seen that there is a striking similarity between the two. Both species show an increase in number during the spring, which later culminates in a large summer maximum. This is followed by a decline and finally there is a small autumnal peak.

Macan (1949), records that at Three Dubs Tarn, in the summer of 1936 (i.e. in July), *Diaptomus gracilis* made up 90 per cent. of the zooplankton. A comparable state was reached here in February 1954 when *Boeckella triarticulata* comprised 70 per cent. of the population.

Some of the genera and a few of the species of phytoplankton and zooplankton collected from Saddle Hill are recorded in papers from Japan, North America, and China. From a pond in Japan, with an oxygen content, pH, and chemical composition of the water similar to those at Saddle Hill, Mizuno (1952) has taken the following:

Euglenophyceae:	*Euglena* sp.
Myxophyceae:	*Oscillatoria* sp.
Bacillariophyceae:	*Synedra* sp.
	Navicula sp.
	Gomphonema sp.
Rotifera:	*Lecane* sp.
	Filinia longiseta
	Keratella sp.
Cladocera:	*Chydorus sphaericus*

Riley (1940) mentions the following from North America:

Chlorophyceae:	*Staurastrum* sp.
	Euglena sp.
Dinophyceae:	*Peridinium* sp.
Myxophyceae:	*Oscillatoria* sp.
Chrysophyceae:	*Mallomonas* sp.
Bacillariophyceae:	*Fragillaria* sp.
	Synedra sp.
	Tabellaria sp.
	Asterionella sp.
Rotifera:	*Keratella quadrata*
	Synchaeta sp.
	Conochiloides sp.
	Filinia longiseta
Cladocera:	*Chydorus sphaericus*

From ponds in Central China, Mashiko (1951*a*, 1951*b*) has recorded the following:

Dinophyceae:	*Peridinium* sp.
Bacillariophyceae:	*Gomphonema* sp.
	Navicula sp.
Protozoa:	*Difflugia corona*
Rotifera:	*Testudinella patina*
	Synchaeta sp.
	Filinia longiseta
	Lecane sp.
	Keratella quadrata
Cladocera:	*Simocephalus vetulus*
	Daphnia carinata
	Alona sp.
	Chydorus sphaericus

It is remarkable that of the six species of rotifer which have been recorded at Saddle Hill, three species and five genera have been reported from Central China.

Mashiko (1953), notes that *Keratella quadrata* is a cold water rotifer which generally appears during the winter months, but at Hankow it was plentiful during the spring—the same season of its occurrence here.

At Hankow, *Difflugia corona* also appeared in spring collections, and was abundant during midsummer but completely absent in the winter.

Even from the consideration of such a small entity as a pond, it is evident that the plankton inhabitants of freshwater show a marked degree of cosmopolitanism, at least to the generic level. This is ascribed to their ability to form resistant stages which are readily dispersed by the wind or carried by birds. In spite of its isolation, the New Zealand zooplankton shows an affinity with the freshwater faunas of Great Britain, North America, and Asia as is clearly indicated by the preceding results.

VII. Acknowledgments

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VIII. References

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Appendix I

THE FAUNA

Protozoa	
Rhizopoda	*Difflugia corona* Wallich
Ciliophora	*Paramoecium caudatum* Ehrenberg
	Stylonichia sp.
	Vorticella sp.
Coelenterata	
Hydrozoa	*Hydra viridissima* Pallas
Platyhelmia	
Turbellaria	*Planaria* sp.
Polyzoa	*Plumatella polymorpha* Kraepelin
Rotifera	*Synchaeta pectinata* Ehrenberg
	Lecane inopinta Harring & Myers
	Testudinella patina (Hermann)
	Keratella quadrata var. *edmondsi* Ahlstrom
	Filinia longiseta (Ehrenberg)
	Conochiloides coenobasis Skorikov
Annelida	
Oligochaeta	*Chaetogaster* sp.
Hirudinea	*Glossiphonia* sp.
Mollusca	
Gasteropoda	*Gyndlachia* sp.
	Potamopyrgus antipodum Gray
	Potamopyrgus sp.
Lamellibranchia	*Corneocyclas* sp.
Arthropoda	
Cladocera	*Daphnia carinata* var. *thomsoni* Sars
	Simocephalus vetulus var. *elizabethae* Sars
	Camptocercus australis Sars
	Chydorus sphaericus (Baird)
	Alona eucostata Sars
	Ilyocryptus sordidus Lieven

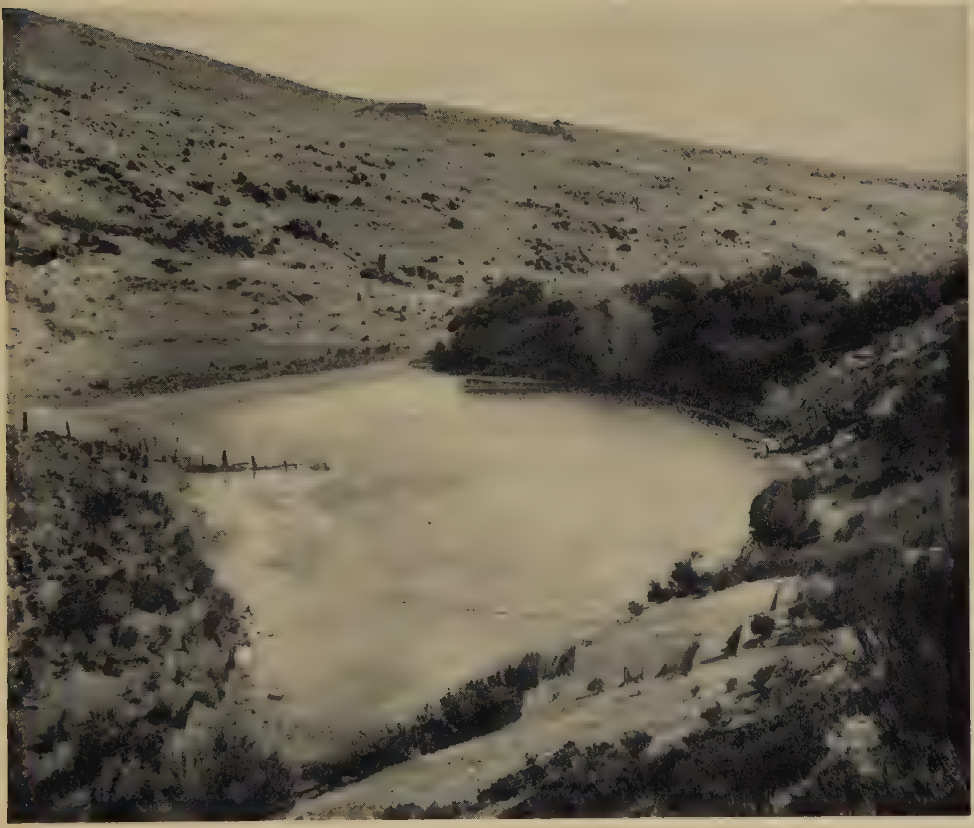
Ostracoda	*Cypridopsis* sp.
	Herpetocypris pascheri Brehm
Copepoda	*Boeckella triarticulata* Thomson
	Cyclops fimbriatus Fischer
	C. viridis Jurine
Insecta	
Odonata	*Aeschna brevistyla* Rambur
	Austrolestes colensonis White
	Xanthocnemis zelandica Selys
Hemiptera	*Microvelia macgregori* Kirkaldy
	Anisops assimilis Buchanan-White
	Sigara arguta Buchanan-White
Trichoptera	Caddis larvae
Coleoptera	*Rhantus pulverosus* Stephens
	Antiporus wakefieldi Sharp
	Enochrus tritus Broun
	Dytiscid larvae
Diptera	*Hydrellia enderbyi* (Hutton)
	Hercostomus argentifacies Parent
	Chironomid larvae 2 spp.
Hydracarina	Hygrobatidae 2 spp.
	Hydrachnidae 1 sp.
Vertebrata	
Amphibia	*Hyla aurea* Lesson
Aves	*Anas superciliosa* Gmelin
	Phalacrocorax carbo L.
	Charadrius bicinctus Jardine & Selby
	Larus dominicanus Lichtenstein

APPENDIX II

THE FLORA

Algae	
Euglenophyceae	*Trachelomonas westii* Wolozy
	Euglena proxima Dang.
	Lepocynclis steinii Lemm.
	Peranema trichophorum Ehr.
	Dinema (griseolum?)
	Urceolus cyclostomatus Stein
Chlorophyceae	*Chlamydomonas* 3 spp.
	Gloeocystis sp.
	Carteria globosa Korsch
	Dispora crucigenioides Printz
	Chaetopeltis orbicularis Berthold
	Uronema elongatum Hodgetts
	Ulothrix spp.
	Stigeoclonium spp.
	Microthamnion kuetzingianum Naeg.
	Aphanochaete repens A. Br.
	Chaetosphaeridium globosum (Nordst.) Klebahn

Chlorophyceae (*continued*)	*Coleochaete scutata* Breb.
	Oedogonium 4 spp.
	Bulbochaete spp.
	Spirogyra spp.
	Debarya spp.
	Zygnema spp.
	Zygnemopsis spp.
	Mougeotia spp.
	Sirogonium spp.
	Cosmarium 3 spp.
	Closterium 2 spp.
	Pleurotaenium ehrenbergianum (Breh.) De Bary
	Staurastrum 2 spp.
	Gonatozygon spp.
	Hormidium spp.
	Colacium (*vesiculosum?*)
	Harpochytrium sp.
Xanthophyceae	*Ophiocytium cochleare* (Eichw.) A. Br.
	Mischococcus confervicola Naeg.
Cryptophyceae	*Cryptomonas* spp.
Dinophyceae	*Peridinium cinctum* Ehr.
Myxophyceae	*Oscillatoria* spp.
	Lyngbya spp.
Chrysophyceae	*Synura uvella* Ehr.
	Chromulina spp.
	Mallomonas spp.
	Ochromonas spp.
	Chrysopyxis bipes Stein
	Phaeothamnion spp. (palmella stage)
Bacillariophyceae	*Fragillaria crotonensis* (Edw.) Kitton.
	Nitzschia spp.
	Gomphonema spp.
	Synedra spp.
	Asterionella sp.
	Navicula 2 spp.
	Tabellaria sp.
Pteridophyta	
Eufilices	*Azolla rubra* L.
Spermaphyta	*Juncus polyanthemos* Buchen
	J. lampocarpus Ehr.
	Carex ternaria Forst.
	Glyceria fluitans R. Br.
	Agrostis tenuis Petrie
	Fuchsia excorticata Linnaeus f.
	Cytisus scoparius Link.
	Ulex europeus L.
	Callitriche stagnalis Scop.



A view of Saddle Hill Pond looking south-west. The east bank is a slope of mudstone; the western side is bordered by a much steeper schist spur.

EXPERIMENTAL STUDIES ON THE ECOLOGY OF INTERTIDAL ENVIRONMENTS AT HERON ISLAND

I. EXCLUSION OF FISH FROM BEACH ROCK

By W. Stephenson* and R. B. Searles†

[*Manuscript received April* 4, 1960]

Summary

The zonation of dominant organisms on the beach rock at Heron Island was reinvestigated following the work of Endean, Stephenson, and Kenny (1956) and three zoning algae were noticed. Field indications suggested the apparent sparsity of the biota was due to the browsing activities of fish.

Fish-proof enclosures were constructed, some containing browsing molluscs, and the fauna and flora therein were compared with the surrounding areas by means of detailed general observation, and by estimation of the chlorophyll concentration per unit area of surface. The results confirmed that browsing fish are the most important single controlling factor.

I. Introduction

Studies on the ecology of intertidal rocks have been carried out in Queensland by Endean, Kenny, and Stephenson (1956) and by Endean, Stephenson, and Kenny (1956). In these papers the ecology of the fauna was stressed rather than that of the flora, which was inevitable in view of the very incomplete knowledge then existing on the marine flora of tropical Australia. Moreover the papers were essentially descriptive and biogeographical.

One of the most striking findings in the earlier work was the difference between the faunistic composition and zonation of the intertidal animals on the mainland compared with those on coral islands at similar latitudes. For example in contrast to a diverse fauna and flora at Yeppoon on the mainland (23° 9′ S.), the beach rock at Heron Island in the Capricorn Group (23° 0′ S.) appears barren, with a sparse fauna and inconspicuous flora (Endean, Stephenson, and Kenny 1956).

Meanwhile three other studies have indicated that the fish population of coral islands may affect the inhabitants of intertidal rocks. First, during work at Low Isles, tooth marks of parrot fish on the beach rock were noted and although it was considered these fish were not a major factor in abrasion of cyclonic debris (Stephenson, Endean, and Bennett 1958, p. 306) they must have some effects upon the sedentary fauna and flora.

Secondly, extensive collections of fish have been made at Heron Island from time to time by two methods. Catches obtained by means of a static fish trap initally by Grant and Stephenson and later by Woodland (unpublished data) showed that the commonest larger fish which were trapped on the inner reef flat and lower beach

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rock were algal feeders. Catches of smaller species on the reef flat made by the use of rotenone at low water by Slack-Smith (unpublished data) again revealed a large proportion of algal feeders.

The Barrier Reef region is an exception to the rule that algae dominate at and just below low water mark, because here the corals dominate at the expense of the algae. It is surprising to find a preponderance of algal feeding fish in a region where algae do not preponderate. Probably the wide expanse of reef flat gives a greater overall amount of algae than is found in a normally sloping rocky shore, so that total area compensates for reduced density.

It is possible that intense browsing by fish reduces the dominance of the algae; this could assist the corals in their competition with algae. In support of this idea, intensive trap-fishing at Heron Island led to greatly reduced catches, and it was strongly suspected that this in turn led to an excessive algal growth in the vicinity of the trap for a period of about two years. Intense browsing on the beach rock algae could partly explain their inconspicuousness. It could also explain the sparsity of the sedentary fauna on the assumption that the animals are removed as juveniles.

Thirdly, underwater observation of fish carried out in a preliminary fashion by one of us (W.S.) and more intensively by Slack-Smith showed that, at high water, several species of fish commonly swam above the Heron Island beach rock, and here "stood on their heads" nibbling at the rock and its algal film.

Collectively these observations suggest that the biotic differences between the intertidal rocks of a mainland beach and the beach rock of a coral cay may be due in part to intensive removal of algae by fish in the latter. The simplest test of this hypothesis is to exclude fish from selected areas of beach rock and observe whether the fauna and flora are altered in any way. The results of such exclusion experiments are detailed below.

As a necessary part of the investigation a detailed study was made of the distribution of organisms in the area of investigation, this representing the ecological norm to which the experimental areas are compared.

II. THE AREA INVESTIGATED

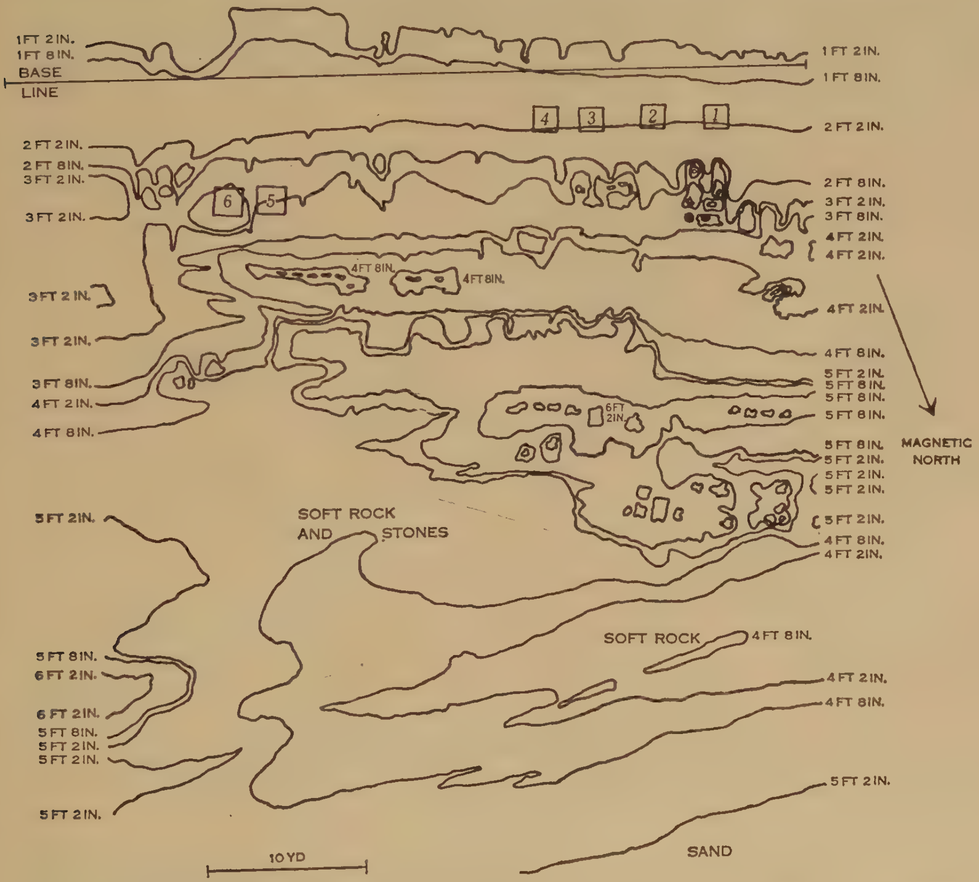
The main investigations were restricted to the 50-yd frontage of beach rock nearest of access to the Marine Laboratory, Heron Island, and were further restricted to the lower portion of the rock which slopes regularly seawards.

(a) *Topography*

A map of the area was prepared by the usual method, using chain and compass, and the beach subdivided into 5-yd squares. Topographical features were interpolated within the squares, and each is accurately placed to within ±1 ft.

Vertical heights upon the beach were determined by recording upon relatively calm days the contour of the water level when this was at a known height. These heights were measured against a vertical tide-pole with 3-in. markings placed at one side of the area; this pole is referred to below as the "beach rock gauge".

On the lower beach vertical measurements are accurate to about ±½ in., but in the upper half only to about ±1 in. The reduced accuracy is due to (i) increased amplitude of waves once the level is too high for the reef crest to give much protection. This makes precise determination of heights on both the gauge and the beach rock far from easy even in a 5-knot wind; and (ii) the fact that the tide moves rapidly over the upper beach which is roughly at mean sea-level so that before a complete contour can be sketched an appreciable movement has occurred. To minimize this source of error only a short portion of a contour was recorded on a given tide, commencing just before a given level had been attained and concluding just after, making judged allowances at either end.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6FT 2IN.
5 FT 8IN.
MAGNETIC NORTH
5 FT 8IN.
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5 FT 2IN.
5 FT 2IN.
4 FT 8IN.
4 FT 2IN.
5FT 2IN.
SOFT ROCK AND STONES
SOFT ROCK
4 FT 8IN.
5 FT 8IN.
6 FT 2IN.
4 FT 2IN.
4 FT 8IN.
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10 YD
SAND

Fig. 1.—Contour map of the beach, with 6-in. contours, based upon an arbitrary pole datum.

The contour map of the beach is given in Figure 1, and general photographs on Plate 1, Figures 1 and 2.

To convert the contour heights, based upon an arbitrary pole datum, into meaningful terms presents difficulties which are partly due to the form of the tidal curve in the reef flat area. Typical curves are given in Figure 2. Only on neap tides is the curve of normal form; on all others the lower portion of the curve is truncated. This is due to the retention of water in the extensive shallow lagoon or reef flat area by the encircling reef crest. The higher parts of this crest reach to the level of low water neaps, but the average level is nearer mean low water. The tide falls normally to a little above mean low water and reaches a "lagoon level" (which is equivalent to the "moat level" in Stephenson, Endean, and Bennett 1958, p. 266). After this it falls very slightly and slowly, being almost stationary for periods of up to 3 hours. The incoming tide, once it has reached the level of the reef crest, rushes in rapidly, making the lower part of the curve asymmetrical. The overall effect is that the low water levels of all tides except neaps differ only by a matter of 2–3 in. The average lagoon level is about 2 ft higher than the mean low water level of spring tides, which is the true local datum.

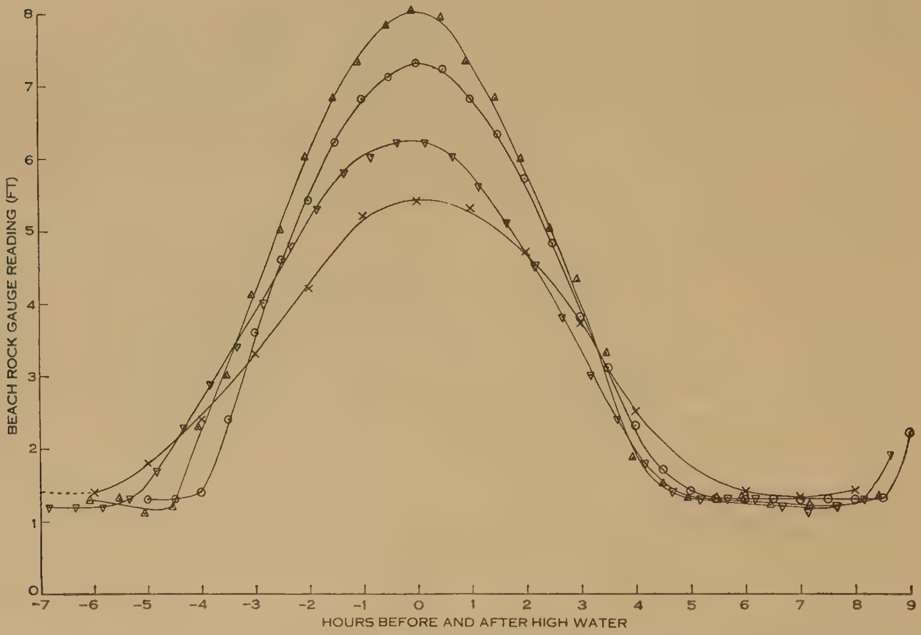

Fig. 2.—Tidal curves on the beach rock gauge ranging from a spring tide (△, 31.i.60) to a neap tide (×, 22.i.60).

The datum taken for present purposes is that of M.L.W.S. in the lagoon immediately adjacent to the beach rock. This is a legitimate datum in that there has been no obvious change in this level in 10 years of casual observation (W.S.).

Time was not available to determine the levels upon the beach rock gauge on a sufficient number of occasions to establish a relationship between observed data and predicted data for a standard port (e.g. Brisbane).

Fortunately a recording and visual tidal gauge had been established in the reef flat area at Heron Island by the Commonwealth Department of Civil Aviation who have most kindly made available their results. It is possible to relate levels on the beach rock gauge with visual levels on this gauge (referred to below as the "recording gauge") and relate the latter to predicted data at Brisbane.

Simultaneous recordings of the two gauges at Heron Island gave the data recorded in Figure 3. Above the 2-ft level on the beach rock gauge, this gauge gave values consistently 1 in. above that of the recording gauge and conversions are simple. Below the 2-ft level the curves diverge, with the beach rock gauge eventually giving readings much higher than the recording gauge. The explanation lies in the local topography. The recording gauge was situated in the main drainage channel from the reef flat, which had been deepened artificially in the 1930's. Here the ease of outward flow of water upon a spring tide evidently allowed a much lower level (*c.* 10 in.) to be attained than at the beach rock gauge approximately ¼ mile away. It is evident that the term "lagoon level" is a partial misnomer. However, even with these complications, it is possible from Figure 3 to convert beach rock levels to equivalent levels on the recording gauge.

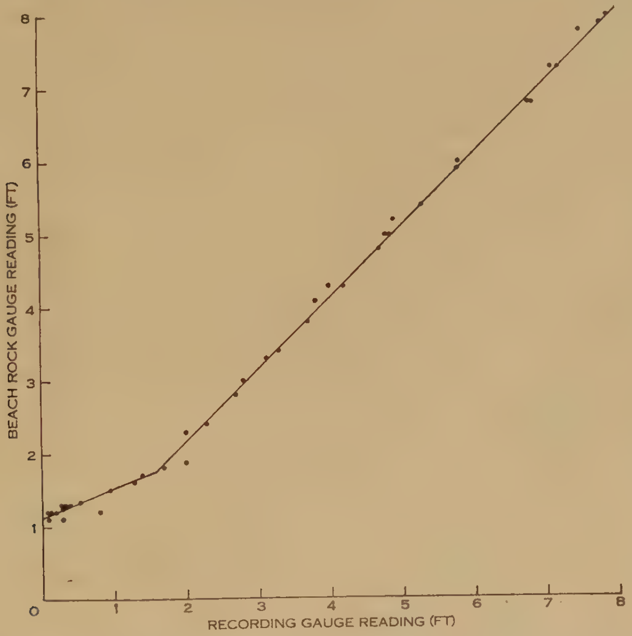

Fig. 3.—Relationship between tidal levels on beach rock and recording gauges. Readings taken at intervals during the second half of January 1960.

To establish a relationship between the recording gauge data and the predicted data for Brisbane, the comparable values of low waters and high waters throughout the months of December 1959 and the first half of January 1960 were plotted against each other as shown in Figure 4. Apart from the lower low waters there is approximately a straight-line relationship.

The Department of Harbours and Marine (1960) at Brisbane have kindly provided the following data about levels at that port: M.H.W.S., 6 ft 7 in.; M.H.W., 5 ft 11 in.; M.H.W.N., 5 ft 3 in.; M.S.L., 3 ft 6 in.; M.L.W.N., 1 ft 11 in.; M.L.W., 1 ft 2 in.; M.L.W.S., 0 ft 6 in. From Figure 4 the equivalent levels at the recording gauge at Heron Island are respectively: 7 ft 2 in., 6 ft 4 in., 5 ft 7 in., 3 ft 5 in., 1 ft 5 in., 0 ft 7 in., and 0 ft 4 in. From Figure 3 the equivalent levels at the beach rock gauge are: M.H.W.S., 7 ft 3 in.; M.H.W., 6 ft 5 in.; M.H.W.N., 5 ft 8 in.; M.S.L., 3 ft 6 in.; M.L.W.N., 1 ft 8 in.; M.L.W., 1 ft 5 in.; M.L.W.S., 1 ft 2 in. This last level is taken as the "local datum" (see earlier).

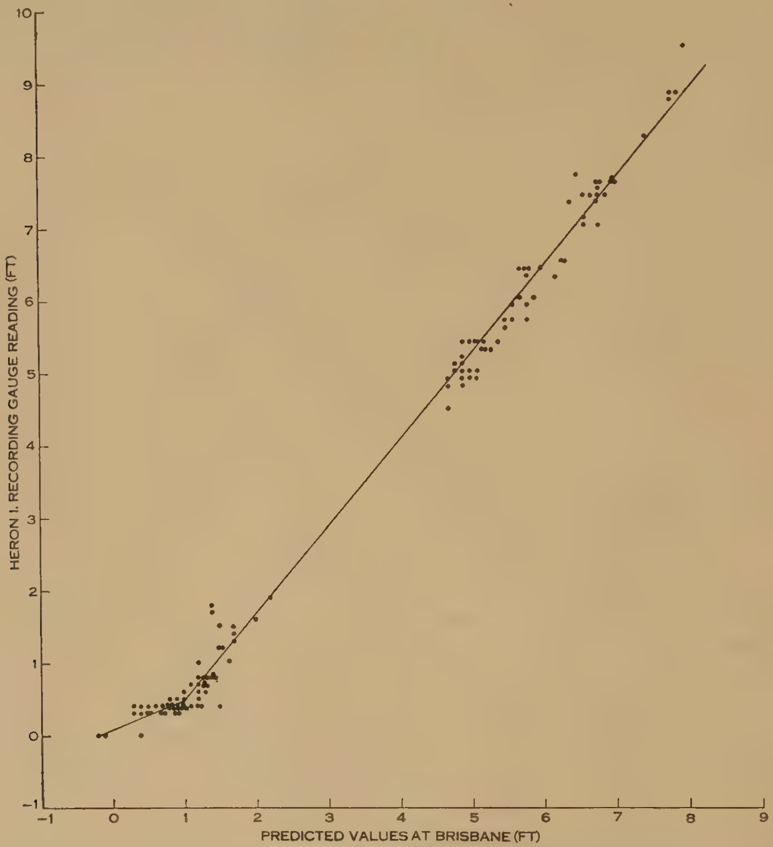

Fig. 4.—Levels of high waters and low waters on the recording gauge plotted against predicted values at Brisbane. Data cover most of December 1959 and the first half of January 1960.

It should be noted that no adjustment of these levels for splash, to give "effective tidal levels", is necessary. The effects of splash are almost eliminated by the protection of the reef crest.

(*b*) *Nature of the Substratum*

Beach rock is a well-known intertidal environment of the warmer seas, and consists, at Heron Island as elsewhere, of poorly assorted sand grains and larger fragments of calcareous material held by a calcareous cement (see Revelle and Fairbridge 1957, p. 258, for a recent review).

Above the area of investigation the uppermost portion of the rock, where it abuts on the beach sand, is friable and poorly consolidated. Immediately below this in the gully region (see Fig. 1) the rock has been broken into numerous stones and boulders distributed somewhat irregularly, some hard and some soft.

In the area investigated the rock was completely consolidated but varied in its apparent hardness and degrees of surface pitting. The hardest rock, as indicated by the difficulty in chiselling and the reactions to a hammer blow, was in the higher regions (part of the *Entophysalis* zone—see below). Here the surface was abundantly pitted with shallow excavations slightly smaller than a finger tip (Plate 1, Fig. 3).

In the middle regions (*Calothrix*-chiton zone—see below) this type of pitting was rarely present, but instead most of the surface bore the abrasion marks of chitons. The surface was not noticeably softer than at the higher levels.

In the lower regions (*Blidingia* zone—see below) the surface was without deep pitting or continuous abrasion marks. The consistency was softer than in the middle levels.

Throughout the area of investigation the strata dip seawards at an angle of *c*. 5° with the major vertical fracture joints running parallel to the beach and with minor joints at right angles serving as drainage channels. The fracture planes are clearest in the upper portion of the beach where roughly flat-topped slabs of rock (15–30 cm thick) remain attached to the lower strata or occasionally have become free. In the regions occupied by chitons (see below) the fracture planes have been excavated and undercut by their abrasive activities (Plate 1, Fig. 4). In the lower portions of the beach, the rocks have flat surfaces with the edges smoothly rounded, and the strata are difficult to distinguish.

Below the beach-rock and separating it from the reef flat proper there is an inshore gutter containing gritty sand above a rock base.

(*c*) *Species Encountered*

Following this section where only one species of a genus is referred to, it is only given its generic name.

(i) *Fauna*.—This differs considerably from that of the previous investigation (Endean, Stephenson, and Kenny 1956, p. 323). The sedentary fauna reported below is more restricted first because the topographically confused upper portion of the rocks was deliberately excluded from the present work, and secondly because, owing to the narrow frontage of the experimental area, the situation differed in detail from the more general picture previously presented. In one case (*Grapsus strigosus*) a species was overlooked in the previous work (Endean, Stephenson, and Kenny 1956, p. 335). Reference is made below to understone and swimming forms not detailed previously, but the listed fauna is incomplete by exclusion of forms not likely to influence the surface of the beach rock (e.g. burrowing bivalves, errant polychaetes).

MOLLUSCA	
LORICATA	*Acanthozostera gemmata* (Blainville)
GASTROPODA	*Cerithium moniliferum* Kiener
	Nerita albicilla L.
	Planaxis sulcatus (Born)
	Siphonaria australis Quoy & Gaimard
ARTHROPODA	
DECAPODA	*Clibanarius virescens* Krauss
	Eriphia laevimana Latreille
	Grapsus strigosus (Herbst)
	Leptodius exaratus (H. M. Edwards)
	Petrolisthes lamarcki (Leach)
CHORDATA	
PISCES (commoner species only)	*Abudefduf coelistinus* (Cuvier)
	A. palmeri (Ogilby)
	A. saxatilis (L.)
	Acentrogobius ornatus (Rüppell)
	Acanthurus dussumieri Valenciennes
	A. mata (Cuvier)
	A. xanthopterus Valenciennes
	Bathygobius fuscus (Rüppell)
	Callogobius hasselti (Bleeker)
	Choerodon albigena (de Vis)
	C. transversalis Whitley
	Eleotriodes longipinnis (Lay & Bennett)
	Gerres oyena (Forskål)
	Micrognathus brevirostris (Rüppell)
	Petroscirtes sp.
	Pomacentrus tripunctatus Cuvier
	Salarias edentulus (Bloch)
	S. meleagris Valenciennes
	Scarus dubius Bennett
	S. fasciatus Valenciennes
	S. ghobban Forskål
	Siganus lineatus (Valenciennes)
	S. oramin (Bloch)
	Sillago ciliata Cuvier
REPTILIA	*Chelonia mydas* (L.)
	Caretta caretta (L.)

Cerithium moniliferum was identified by Dr. D. McMichael and confirmed by Mr. T. Iredale of the Australian Museum, Sydney; the fish identifications are by Woodland and Slack-Smith (unpublished data); and the remaining identifications are by one of us (W.S.).

(ii) *Flora*.—Special attention was paid to the algae as the main organisms under investigation.

ALGAE	
CYANOPHYTA	*Entophysalis deusta* (Meneghini) Drouet & Daily
	Chroococcus sp.
	Synechococcus sp.
	Oscillatoria nigroviridis Thwaites *in* Harvey
	Lyngbya aestuarii Liebman
	Microcoleus chthonoplastes Thuret
	Calothrix crustacea Thuret
	Rivularia atra Roth

CHLOROPHYTA	*Monostroma* sp.
	Enteromorpha 2 spp.
	Blidingia minima (Naegeli *in* Kuetzing) Kylin
	Cladophora sp.
PHAEOPHYTA	*Ectocarpus mitchellae* Harvey
	Colpomenia sinuosa (Roth) Derbes & Solier
RHODOPHYTA	*Erythrotrichia* sp.
LICHENS	
	Verrucaria sp.

Entophysalis deusta and *Blidingia minima* were identified by Dr. A. B. Cribb, Department of Botany, University of Queensland. The remainder were identified by one of us (R.B.S.) from Tilden (1910), Newton (1931), Chapman (1956), and Cribb (1958).

It should be noted that the previous workers (Endean, Stephenson, and Kenny 1956) almost certainly referred to *Blidingia minima* as "*Enteromorpha* spp.".

(*d*) *Zonation*

A dominant organism has been defined as one "present in greater numbers than any other, giving a characteristic facies to the zone occupied" (Endean, Kenny, and Stephenson 1956, p. 100). This concept of dominance depends upon the judgment of the observer and in the present work a zoologist (W.S.) sees different dominant organisms from an algologist (R.B.S.). Hence two complementary zonation patterns are presented below.

(i) *Zoological Zonation.*—From a zoological viewpoint the following three zones are apparent on the open surfaces of the area investigated:

(1) A "bare" zone, extending down to about M.H.W.N. This is the *Entophysalis* and part of the *Calothrix* zones described below.

(2) A chiton zone with *Acanthozostera* dominant, extending from about M.H.W.N. to M.S.L. This is roughly the same as the *Calothrix* zone described below, excepting that within these levels the chitons are restricted to the vicinity of crevices and overhanging rocks.

(3) An algal zone, extending from M.S.L. to just below L.W.S. This is the *Blidingia* zone described below.

Nerita was common on the lower portions of the beach, in the *Blidingia* zone, and is essentially an understone dweller during daytime low waters, being active at night. Various crustaceans (especially *Clibanarius*) were common on the lower beach in the algal zone, and again essentially restricted to the understone habitat.

Siphonaria was present but not common on the open surfaces of the algal zone.

(ii) *Botanical Zonation.*—From an algological viewpoint three zones are apparent, the two uppermost being macroscopically visible only as thin films giving a characteristic coloration to the rocks. The zones are:

(1) *Entophysalis* zone, from about M.H.W. to M.S.L., as a tan to black coloration of the rocks. This species reaches its best development on the broken region of poorly consolidated beach rock shorewards of the main area of investigation, and in adjacent areas with a more typical profile it clearly forms an uppermost zone. *Verrucaria* and *Rivularia* occur in patches amongst the *Entophysalis*, and *Rivularia*

is abundant on the undersides of rocks and ledges. In this broken region the molluscs *Planaxis* and *Cerithium* are present in sufficient numbers to be codominants in the animal population. (In adjacent beaches *Cerithium* is commonest at L.W.S. amongst *Blidingia*.)

(2) *Calothrix* zone, from about M.H.W. to M.S.L., as a thin black or pinkish covering. This species reaches its best development on the harder surfaces of rock in the middle of the beach. Small amounts of *Blidingia* are found in pools and on vertical faces of rocks, and both *Microcoleus* and *Lyngbya* occur in rock crevices. In this zone *Acanthozostera* is clearly the dominant sedentary animal.

(3) *Blidingia* zone, from M.S.L. to just below L.W.S., as a slimy light green mat, with fronds up to about 7 mm long. *Nerita* is common and *Siphonaria* occurs sparsely in this zone.

All three main zoning algae were present at all seasons.

The zoological and botanical concepts are readily harmonized, and in the work below the three zones are referred to as *Entophysalis*, *Calothrix*–chiton, and *Blidingia* zones respectively.

III. Field Indications of Factors Controlling the Beach Rock Populations

In the previous paper (Endean, Stephenson, and Kenny 1956) possible agencies which might be responsible for the paucity of the beach rock populations were mentioned. The present more intensive investigation casts doubts on the importance of most of these, and suggests others of possible importance.

(*a*) *Tidal Levels*

On the basis of mainland experience one would expect a conspicuous algal zone below the effective level of L.W.N. (i.e. the level after adjustment for wave action). On the beach rock this level lies near the base, leaving only a long narrow strip of rock approximately 2 m wide. However, on this strip no dense and varied algal flora was present, but merely the *Blidingia* which extended to higher levels.

(*b*) *Sand Abrasion*

The lower portion of the rock lying below L.W.N. abuts upon an inshore gutter which serves at low water as a drainage channel for water upon the reef flat. In stormy weather with south-easterly winds the water in this channel can carry sufficient grit in suspension in a lateral current to suggest that abrasion of the flora may be important. However, no appearance of sand blasting has been noted on the rocks either during or after heavy weather. Moreover, on the seawards side of the channel, where a roughly equivalent abrasion effect might be expected, various macroscopic species of algae grow vigorously upon the dead portions of coral masses.

(*c*) *Solar Radiation*

In summer the sun is directly overhead, but nevertheless, if radiation was the main controlling factor the intertidal populations should be better developed on the southerly faces of rocks than on the northerly facing slopes. No such effect was observed.

The fact that *Blidingia* extends upwards into the *Calothrix*–chiton zone on vertical faces and in pools, does not indicate other than the normal vertical extension of a species in moist and in shaded microhabitats.

Solar radiation at Heron Island can hardly be more severe than at equivalent mainland localities, and cannot be the major factor responsible for the sparsity of the beach rock populations.

(*d*) *Nature of the Substratum*

In the previous paper (Endean, Stephenson, and Kenny 1956) the rate at which intertidal negro-heads upon the reef crest wear away was advanced as a possible reason for a relative shortage of oysters. Meanwhile work at Low Isles (Stephenson, Endean, and Bennett 1958) has indicated that the removal of rock from coral boulders was mainly due, in that particular habitat, to the activities of *Acanthozostera*. It seems probable that removal of coral rock surfaces in general may be due to biological activities rather than to any inherent instability of the material. Other than at its extreme shoreward edge where the rock appears to be forming, the appearance and physical properties of the beach rock at Heron Island gives no indication of physical or chemical instability.

Artificial substrata in the form of coarse wire netting, cast-iron stakes, wooden stakes, and a certain number of cement bases were provided on a closely adjacent area of the beach rock and on the reef flat, during the course of operating a static fish trap. The stakes were erected 4 years before the beginning of the present work, and were connected by stout wire netting.

Filamentous algae developed abundantly on the continuously submerged portions of the iron stakes and wire netting, but only relatively sparsely upon the intertidal portions of both these substrata and the others (wood and concrete).

The present work began approximately 18 months after the removal of wire netting from the fish trap, and after a further 15 months the situation was as follows:

(1) Submerged iron stakes on inner reef flat: abundant growth of filamentous algae *c.* 1 cm long.

(2) Intertidal iron stakes on inner reef flat (at level of *Blidingia* zone): black encrusting blue-green algae, no *Blidingia*, infrequent coarse tooth marks (see Plate 2, Fig. 1).*

(3) Intertidal wooden stakes on inner reef flat (at level of *Blidingia* and lower *Calothrix* zones): black encrusting blue-green algae, no *Blidingia*, abundant coarse tooth marks (see Plate 2, Fig. 1).

(4) Intertidal iron stakes on beach rock (*Blidingia* zone): as (2) above but no tooth marks noted (Plate 3, Fig. 1).

(5) Intertidal concrete bases on beach rock (*Blidingia* zone): black encrusting filamentous algae, no *Blidingia*, infrequent fine tooth marks (see below, Plate 3, Fig. 1).

* Woodland (personal communication) has stated: "[On the re-erected trap] . . . filamentous algae only grew below M.L.W.S. level: encrusting algae above this level—small scarids (4–5 in.) were frequently seen scraping these upper algae from the stakes when the trap was operating (but not large fish)."

These observations strongly suggest a substratum effect, and of the substrata available *Blidingia* grew only upon beach rock. The blue-green algae on the artificial substrata were removed only from the wooden surfaces, suggesting that hardness of surface may be important.

Further work upon the effect of substratum is obviously desirable, and has been started. Meanwhile it should be noted that the fauna and flora of the artificial environments did not resemble those at an equivalent height on mainland beaches. In particular iron stakes are generally a suitable substratum for the settlement of oysters, and are used commercially for this purpose in Moreton Bay. No growth of oysters was noted on the stakes of the fish trap at Heron Island.

(*e*) *Browsing Animals*

(i) *Benthic Forms*.—With the exception of *Petrolisthes* which feeds upon suspended material, any of the molluscs and decapods previously listed could remove food materials from the rock surface, and probably they all do so.

Several of the species are essentially under-stone dwellers, at least at low-water during daytime, and it is possible that the less widely ranging of these may have detectable effects in the vicinity of stones and crevices. The only observed effects were in the case of *Nerita* whose browsing marks consist of a series of overlapping oval areas each roughly 1–2 cm in diameter (see Plate 3, Fig. 3). The main browsing of *Nerita* appears to be under stones or in shaded situations, and within the experimental site the area of open rock whose algal population was controlled by *Nerita* did not exceed 100 cm^2 per specimen. The infrequency of suitable habitats for *Nerita*, and the resultant infrequency of the species in the experimental area means that the overall effect is negligible.

In one portion of the beach rock about 200 m from the experimental site, the abundance of *Nerita* at about L.W.N. was such that this appeared to be the main controlling influence on both under and upper rock surfaces. Again each *Nerita* appeared to control about 100 cm^2 of upper surface.

Other under-stone or crevice dwelling species have sufficient mobility at specific periods to have a more general effect. These include two crabs, *Grapsus* which moves freely and rapidly over the rocks at low water during both day and night, and *Eriphia* which comes from sizable holes and crevices on the lower beach and perambulates at low water during the night. These crabs appear to feed upon discrete surface particles which are spaced somewhat distantly, and the absence of any concentrated feeding activity means that none can be recognized. The total number of both species over the investigated area is less than 10 specimens, so it is unlikely that they will be of major importance.

Of the forms living on the more open surfaces of the rocks, *Planaxis* and *Cerithium*, while undoubtedly important, lie higher than the area of investigation (but see reference to *Cerithium* in the experimental enclosures).

Small specimens of *Siphonaria* were uncommon in the *Blidingia* zone of the experimental area and had no detectable effect upon the algae. On a portion of beach rock about 200 m distant from the experimental area, where concentrations of up to five individuals for $0 \cdot 1$ m^2 were noted, again the browsing activity was not detectable in face of other agencies.

The most important benthic browser is *Acanthozostera*. During the day these large chitons typically inhabit excavated crevices but during the night, when covered by the tide, most specimens move away and wander for several metres, browsing as they go. Zig-zag tracks up to 5 cm wide are formed in the *Calothrix* area, and upon these the pale surface of rock is bared (Plate 1, Fig. 4; Plate 3, Fig. 2). The older tracks become re-covered with a darker film of *Calothrix*, and after a while are regrazed. The activities of *Acanthozostera* alone would explain the paucity of algae and of other animals from a strip of beach approximately 2 m wide.

In a portion of the beach rock adjacent to the experimental area, a single smaller chiton (*c.* $4 \cdot 5$ mm long) was browsing a discrete and defined area not overlapping with that of other specimens. The area controlled was *c.* $0 \cdot 2$ m^2.

(ii) *Necktonic Forms*.—The following common larger fish have been observed feeding upon materials attached to the beach rock: *Choerodon albigena*, *C. transversalis*, *Scarus dubius*, *S. fasciatus*, *S. ghobban*, *Siganus lineatus*, and *S. oramin* (Stephenson and Slack-Smith, unpublished data).

On almost every tide during daytime shoals of one or another of these species can be observed nibbling at the rock surface. Underwater observation suggests that, of the larger species, the siganids are the most important browsers.

Examination of the stomach contents of scarids caught in the fish trap (Woodland, unpublished data) typically reveals a greenish white paste consisting of calcareous material mixed with microscopic algal fragments. The main food of these species apparently consists of rock scraping from the beach rock, reef crest, and negro-heads.

Similar material was frequently obtained from the stomach of siganids, although fragments of brown foliaceous algae from the reef flat were more commonly present.

Greenish paste was also occasionally present in the stomach of *Choerodon albigena* although apparently this species feeds predominantly upon animal material including fish, crabs, and bivalves (including oysters).

Examination of the rock surfaces reveals an abundance of surface scorings which cannot be due either to physical causes or the activities of benthic organisms. Two types of marks are usually recognizable, the commoner consisting of some 5–7 fine parallel scratches (Plate 2, Fig. 2), and the remainder of deeper more irregular scratches in an approximately paired arrangement (Plate 2, Fig. 3). Both are normally deep enough to bare the white surface of the rock.

The finer scratches occur in the lower *Entophysalis* zone, are extremely common in the *Calothrix* zone, and reach their maximum density in the upper *Blidingia* zone, where they are so common as to create a bare area of rock. In the lower *Blidingia* zone patches of algae are removed in a pattern greatly resembling that of the finer type of scratches, but differing in that the rock surface is not bared, so that no actual scratch marks are visible (Plate 3, Fig. 5). Here the patches removed vary in frequency from 10 to 60 per 10 cm^2.

The coarser scratches occur in the upper portion of the *Calothrix* zone and less frequently below this level. They are also the commonest scratches on the wood and metal stakes on the reef flat (see earlier).

It seems highly probable that the scratch marks and resultant removal of algae are due to fish, the finer marks being the tooth marks of siganids, and the larger ones of scarids. The form of the front teeth in representatives of the two groups is illustrated (Plate 2, Figs. 4 and 5).

In preliminary work during 1950 an attempt was made to remove all specimens of *Acanthozostera* from a strip of beach rock approximately 10 m wide. It was thought that algae perhaps would invade the cleared area, but a year later no effect was detectable. One suspects that two things had occurred, first a lateral movement of adjacent chitons into the area, and second that some controlling factor other than chiton browsing was in operation.

In the present work it was noted that areas in the *Calothrix*–chiton zone where a detectably dark film had grown in the absence of recent chiton browsing frequently bore siganid tooth marks. It seems likely that if chitons were absent from the beach, much the same end result as regards algae would be obtained from the activities of the larger fish.

The smaller fish in the vicinity of the beach rock have been divided by Mr. R. J. Slack-Smith (personal communication) into two main groups:

(1) Resident species permanently inhabiting small pools. In order of abundance these are: *Bathygobius*, *Salarias edentulus*, *Micrognathus*, *Eleotriodes*, *Acentrogobius*, *Callogobius*, *Petroscirtes*, *Abudefduf palmeri*, and *A. coelistinus*. Of these the following are "algal scrapers": *Salarias*, *Abudefduf palmeri*, and *A. coelistinus*. The following apparently nibble algal strands: *Eleotriodes*, *Acentrogobius*, and *Callogobius*.

(2) Species visiting beach rock from reef flat. These comprise *Pomacentrus*, *Abudefduf saxatilis*, *Gerres*, the three listed species of *Acanthurus*, and juvenile *Sillago*. Apart from *Gerres* and *Sillago* all are "algal scrapers".

No markings upon the rocks and no obvious removal of their algae could be related with certainty to the browsing activities of these smaller fish.

In January 1960 during attempts to relate superficial markings of the beach rock either to physical or biological agencies, numbers of freshly made, deep elongate scratches were observed in the experimental area. These ranged in length from *c.* 5 to 30 cm, and in breadth from *c.* 3 to 5 mm (Plate 3, Fig. 4). Even the hardest rock had been deeply scarred, and considerable mechanical force would be necessary to do this. Examination of adjacent areas showed (1) that these marks were concentrated in the smoother and more gradually sloping areas of the beach, and were much sparser in the rougher areas; (2) that the marks could sometimes be resolved into an interrupted track leading from low to high water marks; and (3) that in transverse gullies the marks tended to run parallel to the beach.

The marks are caused by female turtles (*Chelonia* mostly, with a few *Caretta*) which scramble ashore in summer to lay their eggs.

The general conclusions of the present observations are (1) probably the grazing activities of fish are primarily responsible for the paucity of the beach rock fauna and flora; (2) the chitons play a major role only within a restricted range of levels;

(3) *Nerita* only plays a minor role in the experimental area but may be important near low water mark on beaches providing an abundance of crevices; and (4) there appear to be substratum effects which merit separate investigation.

IV. Experimental Work

It was decided to enclose plots of beach rock with wire netting to eliminate the possible effects of fish browsing, and then note subsequent changes. In some of the enclosed areas browsing molluscs were introduced, and in one case a "sunshade" was incorporated to obtain a crude indication of the effects of solar radiation.

It was realized at the outset that the netting enclosure would alter the environment other than purely in the single desired direction, and in particular that some reduction of sunlight was inevitable. It was not realized that the enclosures might alter the turbulence picture in the experimental plots and lead to some accumulation of sediment. Such sediment in the form of grit did accumulate in small quantities, but as far as could be determined did not affect the results.

(*a*) *Design of the Experiments*

Six cages essentially composed of wire netting and each enclosing *c.* 1 m^2 of beach rock were constructed, four in the *Blidingia* zone and two in the *Calothrix*–chiton zone (see Plate 1, Figs. 1 and 2). Each cage was enclosed by a low concrete wall, *c.* 6 cm high and *c.* 15 cm wide. Beach sand was used in making the concrete and wire netting was embedded in the concrete to make a low vertical wall. The concrete was interrupted for *c.* 10 cm to leave a drainage hole covered with wire netting. In all cases part of the enclosure consisted of overlapping portions of netting lightly attached to each other so that they could be detached for sampling within the enclosed area. The individual cages differed in details as given below.

Blidingia *Zone*

Cage 1 ("*sunshade*").—Vertical supports $\frac{3}{8}$ in. galvanized iron piping *c.* 32 cm long; roof of flat wood held *c.* 32 cm above the rock; sides $\frac{1}{2}$ in. galvanized wire netting; access through sides. Eliminates all but small mobile browsers, eliminates almost all direct sunlight.

Cage 2 ("*coarse mesh*").—Frame of $\frac{1}{4}$ in. wire, verticals brazed to a top 15 cm above rock; top and sides 2-in. mesh galvanized wire netting; access through top. Eliminates large browsers, theoretically permits entry of small mobile browsers.

Cage 3 ("*fine mesh with* Nerita").—As cage 2 except $\frac{1}{2}$-in. mesh galvanised wire used, and 12 large *Nerita* originally introduced, together with a stone about the size of a building brick to provide shelter. Theoretically eliminates browsers except those deliberately introduced.

Cage 4 ("*fine mesh*").—As cage 3, but without *Nerita* or stone. Theoretically eliminates browsers.

Calothrix *Zone*

Cage 5 ("*fine mesh*").—As cage 4 but at different level.

Cage 6 ("*fine mesh with chiton*").—As cage 5 but constructed round the resting place and to include a single large *Acanthozostera c.* 8 cm long.

In both zones, the areas adjacent to the cages were regarded as controls.

The cages required little maintenance for 12 months, after which the fine mesh wire needed renewal in cage 5. Between 12 and 15 months the wire in cage 6 corroded away with unexpected rapidity leaving the area unprotected for part of this period.

(*b*) *Methods of Observation*

Observations were made initially and at roughly three-monthly intervals using two methods:

(i) *General Observations.*—Species of plants and animals present were noted, with rough estimates of the percentages of the areas covered by algae and of the numbers and size of animals present. Rough estimates of the thickness of the algal cover were sometimes attempted.

The removal of specimens for laboratory identifications had a proportionally greater effect on the less common species.

(ii) *Determination of the Amount of Chlorophyll Present per Unit Area of Rock.*—The quantitative value of this method depends upon assuming either that the samples from a given area are derived throughout from similar proportions of the same species, or that the amounts of chlorophyll in different species are the same. The results showed that errors from other causes were much more serious.

Samples 5 cm by 5 cm were taken from each area by first removing the surface film whenever possible by scalpel, and then removing the underlying layers of rock with hammer and chisel until layers without any obvious green coloration were exposed. The excavations were usually to a depth exceeding 5 mm. Because rock fragments tended to fly, or if prevented tended to be contaminated by algae from the film outside the given square, the sampling technique has inherent inaccuracies.

The samples were collected into acetone, and kept in darkness until the final assay. Samples not assayed within 4 days of collection were kept for the remaining interval in a refrigerator. The method used involves a slight modification of that of Griffith and Jeffrey (1944), and application of the formula of Comar (1942).

V. Results of the Experimental Work

(*a*) *Species Present and Rough Estimates of Abundance*

The terms "film" and "mat" are used below, the former indicating thin covering, less than 1 mm thick, and the latter a covering more than 1 mm in thickness. The mats always contained a fine sediment consisting of calcareous mud trapped between the filaments, and it was suspected that the relative contribution of algae and sediment differed. Where the latter appeared to predominate the term "muddy mat" is used.

(i) Calothrix–*Chiton Zone*

Results on the upper part of the experimental area are given in Table 1. In the enclosed areas, in 3 months time, the *Calothrix* had increased in thickness from a film to a mat. This applied both in the non-chiton and chiton cages. In the latter the chiton apparently browsed successively the thin films on the same "bare" area in preference to the thicker areas of algae.

After 3 months in the non-chiton cage the film had thickened to a point of near instability, with the surface showing cracks during a midday low water (with the sun almost vertically overhead). By 6 months a considerable area (*c.* 15 per cent.) had become bare, probably as a result of lifting of the film, and *Enteromorpha* had become established on some of the bared area. By 9 months various blue-green algae had become apparent in the *Calothrix* mat, *Enteromorpha* had increased in importance, and a browsing mollusc (*Cerithium*) had appeared in considerable quantity. After a year the *Calothrix* mat, while still thick and containing various blue-green algae, had become reduced in area. The main factor appeared to be the progressive uprolling of loose edges of the mat caused by large numbers of *Cerithium* wedging themselves into the sheltered area so provided. Green algae had taken over an increased area. After 15 months the *Calothrix* had attained its earlier importance and the area occupied by green algae had become correspondingly reduced. Simultaneously there was an unexplained reduction in the *Cerithium* population.

The chiton cage differed in that no cracking of the surface or lifting of the edges of the *Calothrix* mat were noted. The percentage area obviously covered by *Calothrix* decreased progressively during the year, while the bare area browsed by the chiton increased only slightly. The difference was due to the progressive colonization of the bare area by green and red algae. Between 12 and 15 months, cage damage had occurred, and interpretation of results is questionable. It was suspected, as in the non-chiton cage, that *Calothrix* was regaining dominance at the expense of the other algae.

The conclusions are:

(1) In the absence of browsing animals, the *Calothrix* covering grows noticeably thicker and produces an unstable mat.

(2) When areas in the *Calothrix* zone are bared by one means or another, then in the absence of browsing activities by fish *Enteromorpha* or *Erythrotricha* may replace the *Calothrix*.

(3) The chiton *Acanthozostera* feeds upon films of *Calothrix* in preference either to mats of *Calothrix* or to *Enteromorpha* or *Erythrotrichia*. The fluctuations in the area of the *Calothrix* mat do suggest, however, that *Acanthozostera* can feed at least upon the edges of the mat.

(4) A single large caged chiton requires the *Calothrix* growth on *c.* $\frac{1}{3}$ m^2 of beach rock. This compares with *c.* $\frac{1}{5}$ m^2 for a smaller chiton as observed outside the cages.

(5) Conditions in the cage which did not contain the chiton were temporarily suitable for the establishment of *Cerithium*.

(6) In both cages the flora increased in complexity by the addition of blue-green and green algae, but the main species was clearly retaining its dominance after 15 months.

TABLE 1

GENERAL OBSERVATIONS, CALOTHRIX–CHITON ZONE

Date, Interval, and Observers	Control (Open Rock)	Fine Mesh Cage (Cage 5)	Fine Mesh with Chiton (Cage 6)
16.x.58 Initially W.S., R.B.S.	*Calothrix* film very thin with chiton marks in vicinity. Marks of fish browsing abundant	100% *Calothrix* film, none recently browsed	70% *Calothrix* film, 30% bare—browsed by the enclosed *Acanthozostera*
4.xii.58 1½ months R.B.S.	As above	100% *Calothrix* film, possibly thicker than above	70% *Calothrix* film 30% bare Small amount *Blidingia* in pool created during cage construction
9.i.59 3 months W.S.	As above	100% *Calothrix* mat, tending to become unstable and lift	70% *Calothrix* mat 30% bare (i.e. as above but *Calothrix* thicker)
20.iv.59 6 months R.B.S.	As above	80% *Calothrix* mat containing *Oscillatoria*, *Synechococcus*, and *Chroococcus* 15% bare 5% *Enteromorpha* sp. 1 as patches *Synechococcus* present but restricted to concrete walls *Cerithium* probably overlooked	50% *Calothrix* mat, composed as cage 5 50% bare *Synechococcus* on concrete wall *Blidingia* in pool
19.vii.59 9 months R.B.S.	As above	80% *Calothrix* mat composed as above 5% bare 15% *Enteromorpha* and *Erythrotrichia* *Erythrotrichia*, *Monostroma*, and *Enteromorpha* on concrete walls *Cerithium* 30 collected, up to 10 mm long, many left	50% *Calothrix* mat, composition as above 45% bare 5% *Enteromorpha* colonizing bare area *Erythrotrichia* and *Monostroma* on concrete walls

TABLE 1 (*Continued*)

Date, Interval, and Observers	Control (Open Rock)	Fine Mesh Cage (Cage 5)	Fine Mesh with Chiton (Cage 6)
1.x.59 $11\frac{1}{2}$ months W.S.	As above	70% *Calothrix* mat, composition as above 5% bare 25% greens, mostly *Enteromorpha* but including *Monostroma* *Erythrotrichia*, *Monostroma*, and *Enteromorpha* on concrete walls *Cerithium* (50 collected, up to 10 mm long, *c.* 50 left) *Calothrix* mat lifting at edges and here and there well away from rock. *Cerithium* clustered mostly beneath these uplifted edges	30% *Calothrix* mat containing other blue-greens 40% bare 30% greens, mostly *Enteromorpha* but including *Monostroma* *Erythrotrichia*, *Monostroma*, and *Enteromorpha* on concrete walls
12.i.60 15 months W.S.	As above	95% *Calothrix*, mat, tough and thick (3–4 mm), composition as above 5% *Enteromorpha* *Cerithium* 7 only present	(Wire roof of cage considerably damaged in the interval since previous observation) 45% *Calothrix* mat, composition as above, only slightly thicker than control, and with fine tooth marks of fish 50% bare 5% green, mostly *Enteromorpha* with some *Erythrotrichia* (?)

TABLE 2

GENERAL OBSERVATIONS, BLIDINGIA ZONE

Date, Interval, and Observers	Control	Sunshade (Cage 1)	Coarse Mesh (Cage 2)	Fine Mesh with *Nerita* (Cage 3)	Fine Mesh (Cage 4)
16.x.58 Initially W.S., R.B.S.	Thin *Blidingia* mat throughout				
4.xii.58 1½ months R.B.S.	*Blidingia* mat thicker and slightly muddy	*Blidingia* formed muddy mat *Synechococcus*—a few small patches (*Blidingia* thick on underside of roof)	*Blidingia* formed muddy mat *Blidingia* thick on concrete walls	As cage 2	As cage 2
9.i.59 3 months W.S.	*Blidingia* mat thick and pitted with fish browsing marks	As above except roof "clean"	*Blidingia* as above except some pitting of surface, cause unknown	*Blidingia* mat very thick (8–10 mm), and patches lifting in heavy seas	As cage 3
20.iv.59 6 months R.B.S.	As initially	As above	*Blidingia* mat thicker than control	80% very thick mat *Blidingia* 20% very thick *Synechococcus* *Ectocarpus* in small patches (*Synechococcus* on concrete walls)	*Blidingia* slightly thicker than control

TABLE 2 (*Continued*)

Date, Interval, and Observers	Control	Sunshade (Cage 1)	Coarse Mesh (Cage 2)	Fine Mesh with *Nerita* (Cage 3)	Fine Mesh (Cage 4)
19.vii.59 9 months R.B.S.	As initially	*Blidingia* slightly less than control	80% *Blidingia* thicker than control 20% *Enteromorpha* sp. 2, tufts to 10 mm high One small bare patch	85% *Blidingia, Synechococcus, Enteromorpha* sp. 2, and *Oscillatoria* 15% *Chroococcus* (*Synechoccocus* dominating walls) (Anemones probably overlooked)	90% *Blidingia* mat as control 10% *Colpomenia* *Cerithium*, *c.* 150, up to 12 mm long (*Cladophora* on walls, three patches up to 10 mm diam.)
1.x.59 11½ months W.S.	As initially	*Blidingia* forming muddy mat with some pitting, cause unknown	100% *Blidingia* mat, very thick, with probably 3 spp. admixed greens and blue-greens	100% *Blidingia* mat, very thick, with probably 5 spp. admixed greens and blue-greens *Nerita* (8 alive) Sea anemone (brown unident.) 12 specimens, diam. to 2 cm, in mat	90% *Blidingia* mat as control 10% *Colpomenia* up to 20 mm diam. *Cladophora, Enteromorpha,* and *Chroococcus* present *Cerithium*, *c.* 200, up to 15 mm long
12.i.60 15 months W.S.	*Blidingia* mat, thick and pitted with fish browsing marks	As above, mat *c.* 8 mm thick	90% bright green *Blidingia* mat *c.* 2 mm thick with little *Synechococcus* 10% *Blidingia* mat extremely thick (*c.* 1 cm) and lifting off	100% *Blidingia* mat, very thick with probably at least 3 admixed spp. of greens and blue-greens, one green (? *Cladophora*) conspicuous Sea anemones, 12 *Nerita*—8 alive *Cerithium* *c.* 100. 5% only small	*c.* 100% *Blidingia* mat, thick (*c.* 5 mm) and muddy *Cladophora, Enteromorpha,* and *Chroococcus* present *Cerithium* *c.* 200 *Siphonaria* 1, on concrete Anemone 1, on concrete No *Colpomenia*

(7) The replacement of some of the *Calothrix* in the experimental cages by other algae implies that, in the normal environment, while fish browsing reduces the thickness of *Calothrix* it also assists in maintaining the species in a position of complete dominance over the other algae.

(8) An excessive thickness of *Calothrix* restricts the browsing activities of *Acanthozostera* to the barer areas. To maintain a constantly thin film of *Calothrix*, and to maintain a constantly wide area for *Acanthozostera* to browse, would require a great nicety in the adjustment of the populations of the two species. Occasional browsing by fish, particularly in the areas with thickest *Calothrix* growth, introduces an element of balance and maintains the constancy of conditions shown in the natural environment.

(ii) Blidingia *Zone*

Results on the lower part of the experimental area are given in Table 2. In the enclosed areas, in 3 months time, the *Blidingia* mat in all cases had increased in thickness and contained more sediment than the control area.

In the sunshade cage the mat was throughout noticeably muddy, and while thicker than the control, it was suspected to contain less actively growing *Blidingia*. This indicates that while *Blidingia* can live in "complete" shade, such conditions are far from ideal. No species other than *Synechococcus* established themselves in the sunshaded area.

In the remaining cages after 3 months (i.e. by midsummer) there were indications that the *Blidingia* mat had thickened to a point of instability. Bodily lifting of portions of the mat was observed in two cages after heavy seas (cages 3 and 4) while surface pitting indicating a more local removal was observed in another (cage 2).

This was followed at 6 months in two cages (3 and 4) and at 9 months in the remaining cage (2) by the establishment of *Ectocarpus* and *Enteromorpha*, possibly on cleared areas. These algae either covered only small areas or alternatively were only temporarily present, and eventually merged into the *Blidingia* mat, which had meanwhile been colonized by a variety of blue-greens.

As in the *Calothrix*–chiton zone no major change to a new floristic climax had been initiated, although the temporary establishment of *Colpomenia* in cage 4 was noteworthy. *Colpomenia* is a common alga of the submerged reef flat, but has not been noted on the beach rock outside the experimental area. The results indicate that this restriction is not solely related to tidal levels.

During the experiment one-third of the introduced specimens of *Nerita* in cage 3 died. Their grazing activities had produced no noticeable effect. Small numbers of *Cerithium* introduced themselves towards the end of the experiment, and again had no noticeable effect.

The establishment of *Cerithium* in cage 4 parallels its appearance in cage 5 in the *Calothrix*–chiton zone. In the immediate vicinity of the experiment this species is restricted to the upper beach amongst stones and boulders. Some 200 m along the beach rock in an area of irregular profile, it is common over a wide range of levels. It seems probable that the species is normally associated with crevices, boulders, and major irregularities in the rock surface. Possibly the experimental cages act as an irregularity in the surface and provide a suitable environment. It should be noted that, at their first appearance in a given cage, the *Cerithium* are quite large (*c.* 15 mm long) and are possibly introduced bodily from other areas as a result of wave action.

In cages where it occurred abundantly *Cerithium* appeared to reduce the amounts of algae present, but in two different ways. In the *Blidingia* zone (cage 4) the effect seemed to be a pure browsing one, whereas in the *Calothrix*–chiton zone (cage 5) the main effect appeared to be by uplifting the edges of the mat of blue-green algae, and making them "flappy".

TABLE 3

RESULTS OF CHLOROPHYLL DETERMINATIONS

Mean results are given in mg/25 cm², with the number of determinations in parentheses

Incomplete results are due to partial loss of samples during transport

Zone and Sample	4.ix.58	9.i.59	20.iv.59	19.vii.59	1.x.59	9.i.60	Weighted Means
Blidingia Zone							
Control	0·61 (1)	0·38 (1)	0·53 (3)	0·53 (3)	0·61 (3)	0·87 (3)	0·62
Sunshade (cage 1)	0·63 (1)	0·27 (1)	0·43 (3)	0·45 (3)	0·45 (3)	0·79 (3)	0·42
Coarse mesh (cage 2)	0·82 (1)	—	0·82 (2)	0·85 (3)	0·86 (3)	0·62 (3)	0·79
Fine mesh with *Nerita* (cage 3)	0·56 (1)	0·53 (1)	0·61 (3)	0·79 (3)	0·86 (3)	0·98 (3)	0·77
Fine mesh (cage 4)	0·63 (1)	0·43 (1)	0·40 (3)	0·55 (3)	0·41 (3)	1·17 (3)	0·62
Calothrix–chiton zone							
Control	—	0·26 (1)	0·43 (3)	0·41 (3)	0·32 (3)	0·59 (3)	0·38
Fine mesh (cage 5)	—	0·49 (1)	0·36 (3)	0·30 (3)	0·49 (3)	0·85 (2)	0·43
Fine mesh with chiton (cage 6)	—	0·21 (1)*	0·40 (3)*	0·25 (3)*	0·57 (3)†	0·36 (2)	0·38

* From chiton-browsed areas.

† 0·19 from chiton-browsed areas.

The establishment of sea anemones in cage 2 is of interest. The randomness of this occurrence could be explained in part by assuming asexual reproduction from a single settled individual. The temporary existence of bared areas could allow for settlement, and the subsequent re-expansion of the thick mat (to surround completely the contracted anemones apart from their oral areas) could provide a suitably moist microhabitat for their continued existence.

(*b*) *Chlorophyll Determinations*

The above results (see Tables 1 and 2) show that the algal population within a given cage tended to become heterogeneous with the passage of time. In the earlier work a single sample was collected from each area for chlorophyll determinations, but later they were obtained in triplicate. The mean results, which are given in Table 3, do not give an accurate picture because there was a large subjective element in the selection of samples. It was thought unwise to take larger or more numerous samples because of the risk of upsetting the entire experiment by clearing too much surface. Even the samples in triplicate introduced this risk, although it was noted that such areas were generally well recolonized by the dominant alga in each cage after a period of 3 months, and scarcely detectable after 6 months.

To simplify discussion of the results a high concentration of chlorophyll per unit area is referred to below as a high algal density. The results in the *Calothrix*–chiton zone show:

(1) In the cage excluding chitons, prior to the establishment of *Cerithium*, the algal density became higher than the control; and

(2) during the period when *Cerithium* was present in numbers algal density decreased but after their disappearance it again became higher than the control.

The individual determinations also showed that the algal density in the chiton-browsed portion within cage 6 was at all times less than in the control.

The results in the *Blidingia* zone show:

(1) In absence of direct sunlight and browsers the algal density is less than that of the controls. Probably lack of browsing does not compensate for a reduction in illumination.

(2) In the fine-mesh cage in which *Cerithium* became abundantly established the algal density became roughly equivalent to that in the control. A population density of *c.* 200 *Cerithium* per m^2 is concluded to have a browsing effect roughly equivalent to the effect of the natural fauna at this level.

(3) Browsing by *c.* 10 *Nerita* had no obvious effect.

(4) Enclosure by coarse mesh results in a marked increase in algal density as compared with the other sampled areas. This indicates that organisms which are excluded by coarse wire are the major controlling influence. These would include the larger fish, and possibly also the smaller fish which, while they could enter, were probably deterred from doing so.

It should be stressed that the difference between the coarse and fine mesh cages is not attributed to the coarseness of the mesh as such, but rather because in the fine mesh cages browsing molluscs were either introduced deliberately or introduced themselves.

VI. RETURN TO NORMAL AFTER DESTRUCTION OF EXPERIMENTAL ENCLOSURES

In mid January 1960 wire was removed from all cages, and the concrete walls were also removed where physically possible (cages 5 and 6 only). Daily observations were made upon the previously protected areas.

In the upper cages (5 and 6) within 24 hours the *Calothrix* mats had become more desiccated than previously. A strong wind (*c.* 25 knots) was believed to be responsible, and this suggests that the enclosures had partly acted as wind shields.

In the lower cages (1–4) within 24 hours a reduction in the muddiness of the *Blidingia* mat had occurred. A similar but less obvious effect could be detected in the surrounding control areas, wave action being responsible. These results suggest that the lower enclosures had partly acted as shelters from wave action.

Within 48 hours the fine marks caused by browsing of siganids were visible in all cages. These were denser in the uppermost cage (5) than in the lower cages (1–4). It appeared that browsing was most intense upon relatively loose portions of the algal mats.

During the remaining week of observation, it was evident that browsing had continued throughout. Siganid tooth marks were then $\frac{1}{2}$–$\frac{2}{3}$ as numerous as in the surrounding control areas.

VII. Discussion

The present work indicates quite clearly that the main factor responsible for the paucity of the beach rock biota is the intense browsing of fish. The only other case of an important effect of fish upon the benthos which is known to the authors is Randall's observations (personal communication) in mid-Pacific lagoons. Here acanthurids controlled the algal density by intensive grazing. In the present case siganids are the most important of the numerous grazing fish.

At its appropriate level the chiton *Acanthozostera* has an important effect, but it is necessary to involve fish to explain the observed constancy in the interrelations of *Acanthozostera* and *Calothrix* (see Section V(*a*)(i), conclusion (8)).

It is unlikely that *Nerita* has important effects, at least in the experimental area, where only *c.* 200 individuals were observed on a 50-m frontage. *Cerithium* can control the algal population, at least temporarily, granted that other conditions are suitable for its establishment and maintenance. These conditions were not found on the control portions of the experimental area.

In absence of browsing activity, the algal cover increases in thickness, becomes unstable, and is removed to give bare areas. These are mostly recolonized by the original species, but some green and red algae enter, at least for a while. In one case an alga typical of the reef flat (*Colpomenia*) and in another a sea anemone became established.

The chlorophyll results, while open to criticism, confirm the general conclusions just given.

During the present experiments while there was an increase in the standing crop of algal material, and an increase in floristic diversity, there was no indication that events were moving towards a different biotic climax. No real explanation has been found why the fauna and flora of the Heron Island beach rock differs from that of the mainland.

The appearance of "exotic" species of algae was most noticeable on the inner vertical concrete walls of the enclosures, suggesting that the nature of the substratum may have important effects. Observations upon other unnatural substrata support this concept, and further experiments are in progress.

In previous work at Heron Island, marked differences in the zonation upon the beach rock and the boulders of the reef crest were noted (Endean, Stephenson, and Kenny 1956). It was thought that the severity of physico-chemical conditions was responsible for the paucity of the beach rock fauna, but as stated above, the browsing activities of fish are more likely to be responsible. If so, the question arises whether the richer fauna of the reef crest boulders could be due to a reduction in this browsing intensity. Field observations of the fish fauna support this view. At low water the tusk fish (*Choerodon albigena*), some of the scarids, and occasionally the siganids,* are concentrated in shallow water either on the reef crest (neap tides) or in the outer parts of the reef flat (spring tides). By the time the middle and upper portions of the isolated reef crest boulders have become submerged most of these fish have moved inshore. This is entirely understandable because any fish which remained on the reef crest would be open to attack by larger predators and especially sharks. The habit of certain of the browsing fish of apparently concentrating their activities to times and situations where there is a shallow cover of water means that the upper portions of the boulders escape most of their activities. This is suggested as an explanation for the dominance of barnacles (*Tetraclita vitiata* Darwin) and oysters (*Crassostrea amasa* Iredale) on boulders. Further experimental work is needed before this explanation can be put forward at all firmly, and this is in progress.

VIII. Acknowledgments

The authors are indebted to the Commonwealth Research Grants of the University of Queensland for financial support, to Mr. R. Kenny for assistance in the construction of the experimental cages, and to Messrs. B. Campbell and W. Stephenson, jnr. for help in surveying. Messrs. R. J. Slack-Smith and D. Woodland offered constructive criticism of the manuscript and most kindly gave permission for the incorporation of some of their unpublished work. Sincere thanks are also due to the Commonwealth Department of Civil Aviation for permission to use their data from the recording tidal gauge at Heron Island, and to the Queensland State Department of Harbours and Marine for information on tidal levels at Brisbane.

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* Siganids normally concentrate at low water in the deeper pools of the reef flat (Woodland, personal communication).

INTERTIDAL ENVIRONMENTS AT HERON ISLAND. I

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INTERTIDAL ENVIRONMENTS AT HERON ISLAND. I

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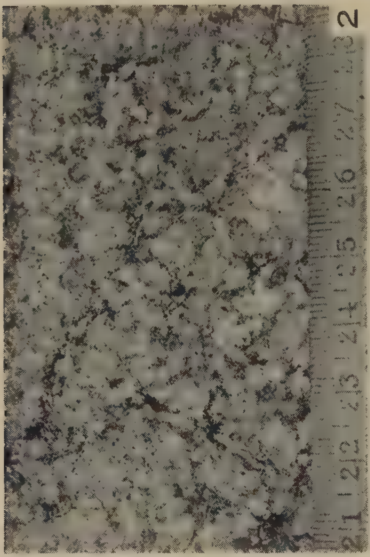
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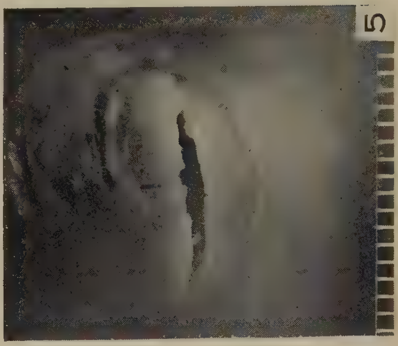
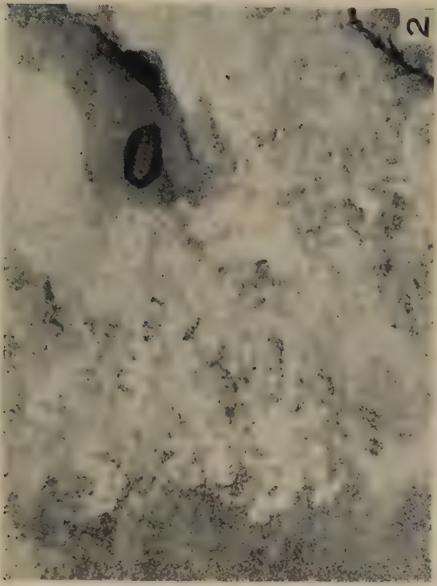


INTERTIDAL ENVIRONMENTS AT HERON ISLAND. I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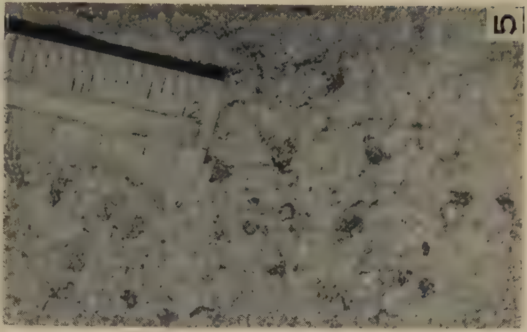
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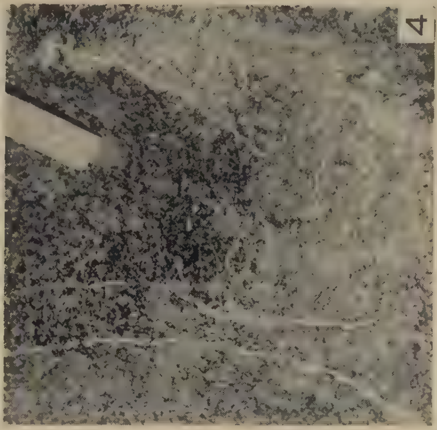
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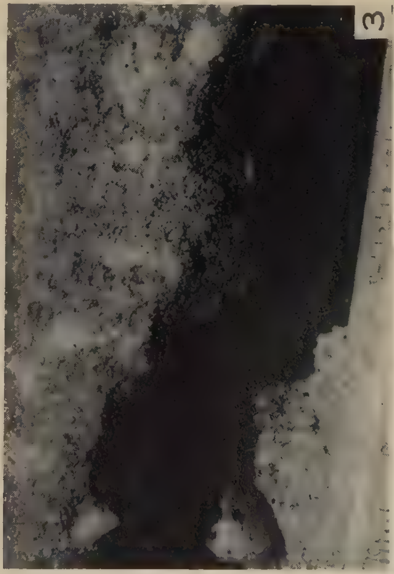
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EXPLANATION OF PLATES 1–3

PLATE 1

Fig. 1.—General view of beach rock from upper *Calothrix*–chiton zone looking west showing lower experimental cages 1–4.

Fig. 2.—General view of beach rock from upper *Calothrix*–chiton zone looking south-east showing experimental cages 5 and 6.

Fig. 3.—Sculpturing of rock surface in *Entophysalis* zone.

Fig. 4.—Chiton-occupied crevice, showing excavation between strata.

PLATE 2

Fig. 1.—Intertidal stakes from reef flat with dark algal growth. On left wooden stake with numerous scratch marks, on right cast iron stakes, each *c.* 5 cm across.

Fig. 2.—Commonest type of surface scratch marks (siganids).

Fig. 3.—Deep irregular surface scratches with approximately paired arrangement (scarids).

Fig. 4.—View of the teeth of *Siganus chrysospilos* (Bleeker). Scale division 1 mm.

Fig. 5.—View of the teeth of *Callyodon dubius* (Bennett). Scale divisions 1 mm.

PLATE 3

Fig. 1.—Cast iron stake cemented into beach rock, showing relative densities of dark-coloured algae on the three substrata. The lightest peripheral material is beach rock.

Fig. 2.—Browsing marks of chiton; the specimen is approximately 7 cm long.

Fig. 3.—*Nerita albicilla* with characteristic browsing marks, showing light on dark background.

Fig. 4.—Long scratches on beach rock caused by turtles, "background" marks mostly caused by siganids.

Fig. 5.—Pattern of removal of *Blidingia* in the lower half of its zone. Removed areas are darker coloured and the rock surface is not exposed.

SEA-LEVELS AROUND AUSTRALIA DURING THE INTERNATIONAL GEOPHYSICAL YEAR

By B. V. Hamon* and F. D. Stacey†

[*Manuscript received June* 6, 1960]

Summary

The variations in mean sea-level observed at Australian tide-recording stations during the International Geophysical Year are presented in graphical form and compared with the changes in density of sea-water measured near some of the stations. The observations are in general but not detailed agreement with the isostatic hypothesis according to which sea-level and water density are directly related.

I. Introduction

Tide gauges are operated at most Australian ports, and during the International Geophysical Year monthly mean sea-levels were computed from the records obtained from a number of the gauges selected, as far as possible, for their freedom from local influences of harbours and estuaries. Several gauges were set up specially to obtain records for the International Geophysical Year at more exposed stations, where it was thought that the sea-levels recorded would better represent the open ocean.

All the monthly mean sea-levels have been published (Union Géodésique et Géophysique Internationale 1959). The International Geophysical Year programme also included regular determinations, from temperature and salinity measurements, of the density of the sea-water at some of the stations. In this paper the variations in sea-level are compared graphically and the correlation with changes in density of the sea-water at six of the stations is examined. A preliminary assessment is made of the extent to which the sea-level around Australia is isostatic.

Some of the positions at which gauges were set up specially for the International Geophysical Year proved to be too exposed, but these gauges are being maintained because the records from these exposed island stations may prove useful at a later date. Stations from which the records were not sufficiently continuous and reliable have been omitted from this paper.

II. Tide Gauge Stations

Figure 1 shows the geographical positions of the tide gauge stations used. The gauges at Maatsuyker Island, Cape Sorell, Port Moresby, and Eden were specially installed for the International Geophysical Year; the others were selected from those normally operated by port authorities. The selection is a compromise between good geographic coverage and the avoidance of stations at which wind or freshwater discharge might have important effects. Of the 18 stations used in this

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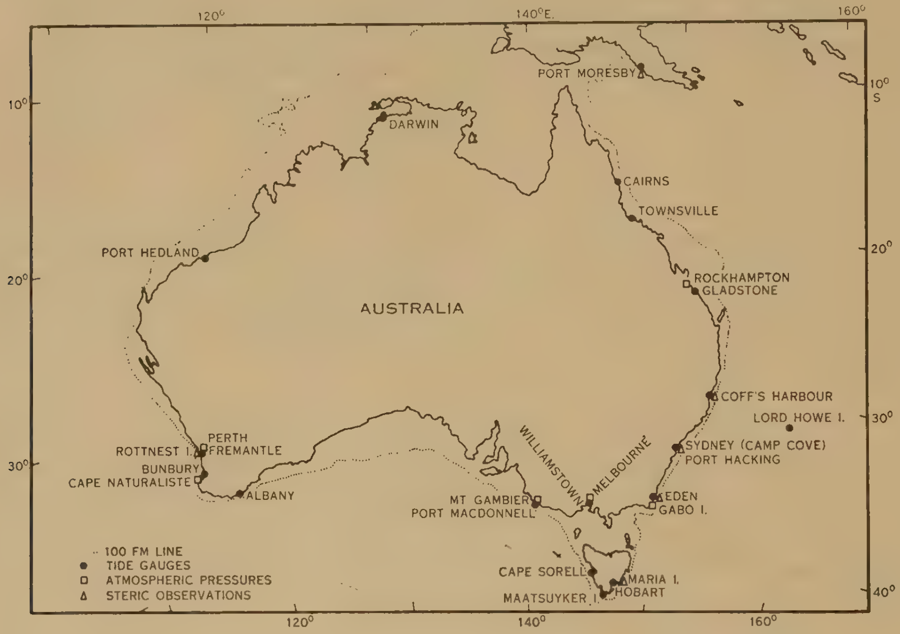
paper, one (Hobart) may be affected by river discharge in months of extreme rainfall (see Section IV) and three (Darwin, Williamstown, and Port Hedland) are near large areas of shallow water in which the piling up of water by wind might be expected.

During part of the International Geophysical Year a tide gauge was operated at Rottnest Island where the changes in sea-level over the period February to July 1958 showed very close agreement with the changes at Fremantle. This indicates that the Fremantle levels are not seriously influenced by freshwater discharge from the Swan River.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PORT MORESBY
DARWIN
CAIRNS
TOWNSVILLE
PORT HEDLAND
ROCKHAMPTON
GLADSTONE
AUSTRALIA
COFF'S HARBOUR
LORD HOWE I.
PERTH
ROTTNEST I.
FREMANTLE
BUNBURY
CAPE NATURALISTE
ALBANY
WILLIAMSTOWN
MELBOURNE
SYDNEY (CAMP COVE)
PORT HACKING
EDEN
GABO I.
MT GAMBIER
PORT MACDONNELL
CAPE SORELL
MARIA I.
HOBART
MAATSUYKER I.
100 FM LINE
● TIDE GAUGES
◻ ATMOSPHERIC PRESSURES
△ STERIC OBSERVATIONS

Fig. 1.—Locations of tide gauges, steric (or water density) observations, and atmospheric pressure stations (where these differ from the tide gauge locations).

The monthly mean levels at Port Moresby, Cape Sorell, Maatsuyker Island, Rottnest Island, Camp Cove, and Port MacDonnell have been computed from hourly levels. Mean levels at the other stations are averages of high and low water (or mean tide level). Rossiter (1958) showed that mean tide level may differ appreciably from the mean sea-level obtained from hourly values, particularly where shallow water tidal components have significant amplitudes. However, at any station the difference should be approximately constant from month to month so that differences in mean tide level at one station should be directly comparable with differences in mean sea-level at another. Both mean tide levels and mean sea-levels were computed for Camp Cove for the International Geophysical Year period. The differences (monthly mean tide level minus monthly mean sea-level) had a mean value of +0·3 cm, with a standard deviation of 0·3 cm. Similar differences have been noticed in levels at Hobart for the period January to June 1956.

There are two tide gauges in Sydney Harbour (Port Jackson). The one at Camp Cove, just inside the entrance to the harbour, was chosen for the International Geophysical Year. The standard gauge is at Fort Denison, 6 miles from the harbour entrance. The difference between monthly means obtained from the two gauges is negligible.* Previously published mean tide levels for Sydney (Union Géodésique et Géophysique Internationale 1940, 1950) were obtained from the Fort Denison gauge.

At each station the monthly mean sea-level was simultaneously adjusted to compensate for changes in atmospheric pressure (Section III) and for the arbitrary datum level of the tide gauge, by adding the mean atmospheric pressure (in mb) to the mean sea-level (in cm) for each month, and then subtracting from the sum for each month the mean value of this sum over the whole period of observation.

In the following six cases the tide gauge and barometer were separated by some distance:

Tide Gauge	*Barometer*
Fremantle	Perth
Bunbury	Cape Naturaliste
Port MacDonnell	Mt. Gambier
Williamstown	Melbourne
Eden	Gabo Island
Gladstone	Rockhampton

III. The Isostatic Hypothesis

On the basis of a global survey of seasonal changes in sea-level, Pattullo *et al.* (1955) suggested that sea-level was approximately isostatic, i.e. that the total pressure on the deep sea floor is independent of time. This implies that the sea-level at any point depends upon two variables only; atmospheric pressure and the mean density of a column of water from the surface to the sea floor. In this paper the Australian sea-level data for the International Geophysical Year are examined in the light of this hypothesis.

Atmospheric pressure has a direct effect on sea-level; one millibar increase in atmospheric pressure results in a lowering of sea-level by one centimetre. Using the monthly mean atmospheric pressures listed in the monthly statistical summary of the Australian Bureau of Meteorology for 1957–58, all the measured sea-levels have been adjusted to compensate for the effect of atmospheric pressure at each station. If sea-level is isostatic the adjusted levels thus obtained should depend only on the density of the water.

IV. The Adjusted Sea-Levels

The mean sea-levels, adjusted for variations in atmospheric pressure, are shown in Figure 2. There is a distinct seasonal variation with a maximum in autumn and minimum in spring, as observed by Pattullo *et al.* (1955), and a particularly

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* The mean differences and standard deviations (Camp Cove monthly mean sea-level minus Fort Denison monthly mean sea-level) for the International Geophysical Year period were respectively +0·09 cm and 0·8 cm.

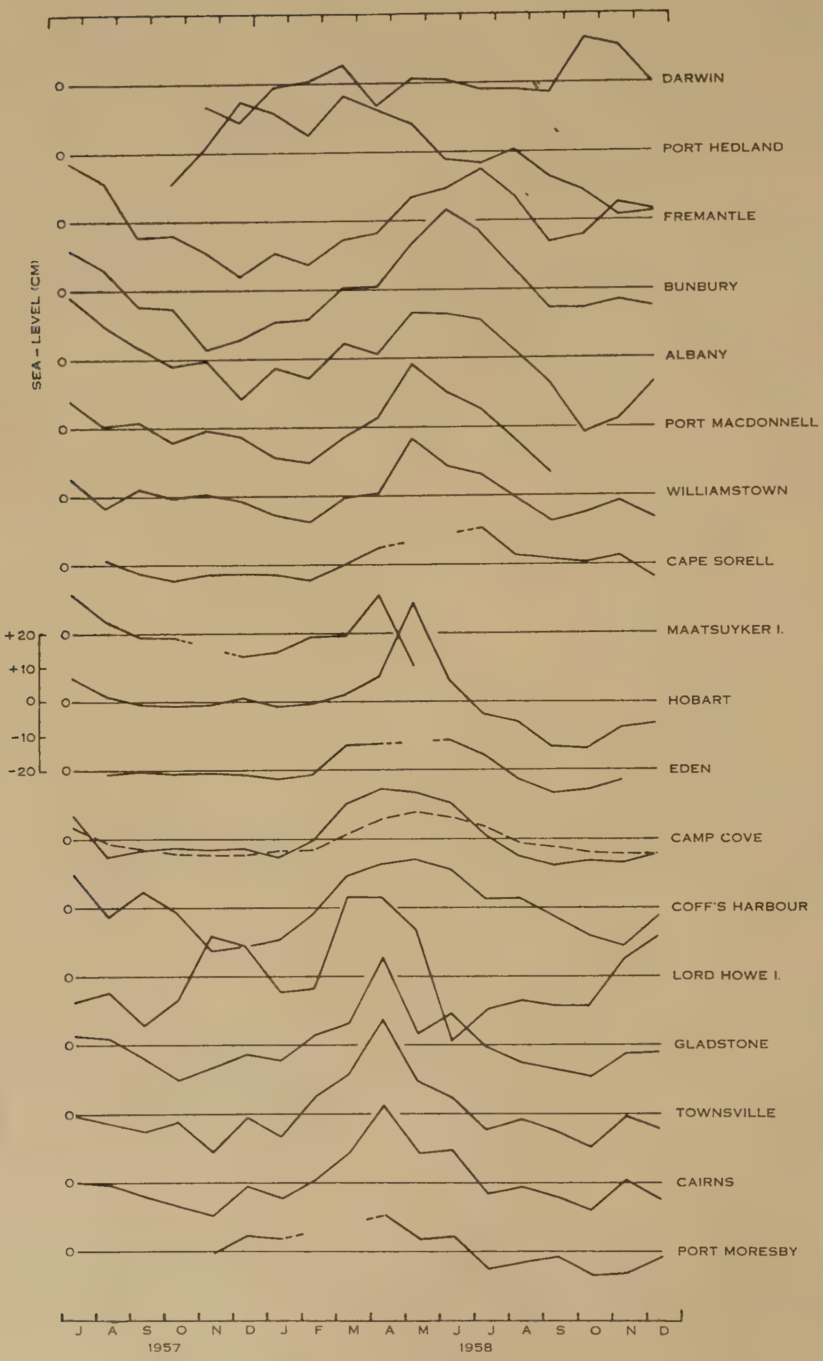

Fig. 2.—Relative values of sea-level, adjusted for variations in atmospheric pressure. The dashed curve shows the long-term mean seasonal variation in adjusted sea-level at Sydney.

strong correlation between sea-levels at neighbouring ports. The long-term average monthly values of corrected sea-level at Sydney are shown also in Figure 2, for comparison with the Camp Cove levels during the International Geophysical Year. It is seen that the seasonal variation in level at Camp Cove during the International Geophysical Year was greater than average, and that the highest level occurred about one month earlier.

The curves for Darwin, Port Hedland, and Lord Howe Island are significantly different from the other curves in Figure 2. At Darwin there was no marked seasonal effect during the International Geophysical Year, while the highest level at Port Hedland occurred five or six months earlier than the highest level at Fremantle.

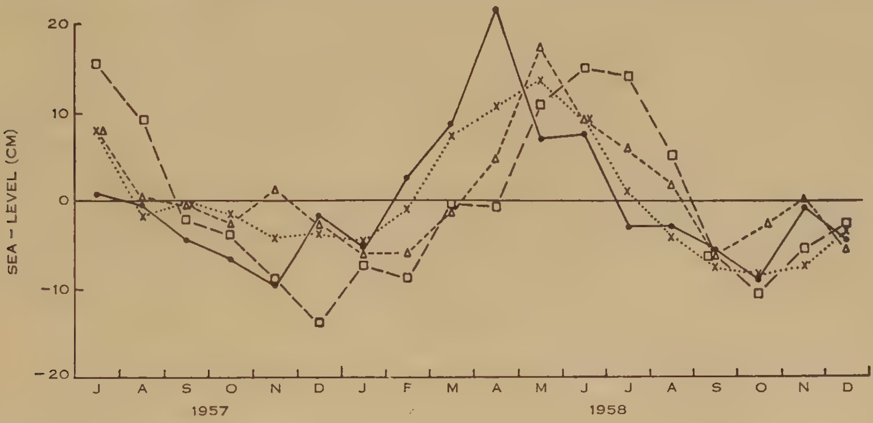

Fig. 3.—Group means of adjusted sea-levels.

●———● Port Moresby, Cairns, Townsville, Gladstone.

×······× Coff's Harbour, Camp Cove, Eden, Hobart (excluding May 1958).

△– – – –△ Maatsuyker Island, Cape Sorell, Port MacDonnell, Williamstown.

□ – – –□ Albany, Bunbury, Fremantle.

The curve for Lord Howe Island shows more variation than any other and, except for the rise in sea-level between February and March, shows little correlation with the sea-levels on the mainland. Similar behaviour has been noted in Japan (Shoji 1957) where the sea-level changes at the island of Hachijo Jima were found to be much larger than those on the neighbouring Japanese mainland.

The unusually high mean sea-level at Hobart in May 1958 appears to be due to fresh water discharge into the Derwent River estuary. The highest May rainfall on record at Hobart occurred in this month. The decrease in sea-level at Maatsuyker Island between April and May 1958 was not apparent at any of the neighbouring gauges. The May level at Maatsuyker Island must therefore be regarded as doubtful, although checks of the records and calculations did not reveal an error.

The similarity of the curves for Port MacDonnell and Williamstown indicates that the Williamstown levels are not as much influenced by the piling up of water by local winds as might have been expected from the extent of the shallow water separating it from the open sea.

By grouping the stations geographically (except Darwin, Port Hedland, and Lord Howe Island) and averaging the adjusted sea-levels in each group (Fig. 3), the variations in adjusted sea-level around Australia in the International Geophysical Year period can be seen more clearly. The amplitude of the seasonal variation in level was approximately the same for each group but the changes occurred later off the south-east coast than off Papua, and later still off the south-west coast. The greater lag of seasonal changes at higher latitudes was noted by Pattullo *et al.* (1955). The lag between the south-west and south-east coasts may not occur regularly. It was noted above that the changes at Camp Cove were earlier during the International Geophysical Year than is indicated by the long-term average monthly sea-level.

TABLE 1

STERIC SEA-LEVEL STATIONS

Tide Gauge	Steric Sea-level Station	Sampling Method	Sampling Depths (m)	Approximate Interval between Samples (Weeks)
Fremantle (32° 10′ S., 115° 48′ E.)	Rottnest I. (32° 2′ S., 114° 53′ E.)	Temperature–chlorinity bridge (*in situ*)	0, 5, 10, 15, 20, 30, 40, 50, 60, 70, 80	4
Pt. Moresby (9° 29′ S., 147° 8′ E.)	Pt. Moresby* (9° 33′ 30″ S., 147° 5′ 56″ E.)	As for Fremantle	0, 5, 10, 15, 20, 30, 40, 50, 60, 70, 80	4
Hobart (42° 50′ S., 147° 19′ E.)	Maria I. (42° 36′ S., 148° 16′ E.)	Nansen bottle	0, 10, 20, 30, 40, 50	2
Camp Cove (33° 53′ S., 151° 15′ E.)	Pt. Hacking (34° 5′ 30″ S., 151° 15′ 30″ E.)	Nansen bottle	0, 10, 20, 30, 40, 50, 75, 100	1
Coff's Harbour (30° 21′ S., 153° 2′ E.)	Coff's Harbour (30° 17′ S., 153° 16′ E.)	Nansen bottle	0, 10, 20, 30, 40, 50	4
Lord Howe I. (31° 31′ S., 159° 7′ E.)	Within *c.* 20 miles of Lord Howe I.	Engine room intake	Surface	6
Eden (37° 5′ S., 149° 59′ E.)	Eden (24 mile stn.) (37° 04′ S., 150° 34′ E.)	Nansen bottle	0, 25, 50, 75, 100, 150, 200, 300, 500	1

* Steric observations for February and March 1958 were taken at 9° 36′ 0″ S., 147° 15′ 30″ E.

The high correlation between variations in sea-level (adjusted for atmospheric pressure) at ports a few hundred kilometres apart is well established. Correlation over much greater distances does not seem to have been studied but the curves of Figure 3 suggest that it may be significant over distances of several thousand kilometres. This possibility could be examined by a careful analysis of residuals after subtracting the long-term mean seasonal variation.

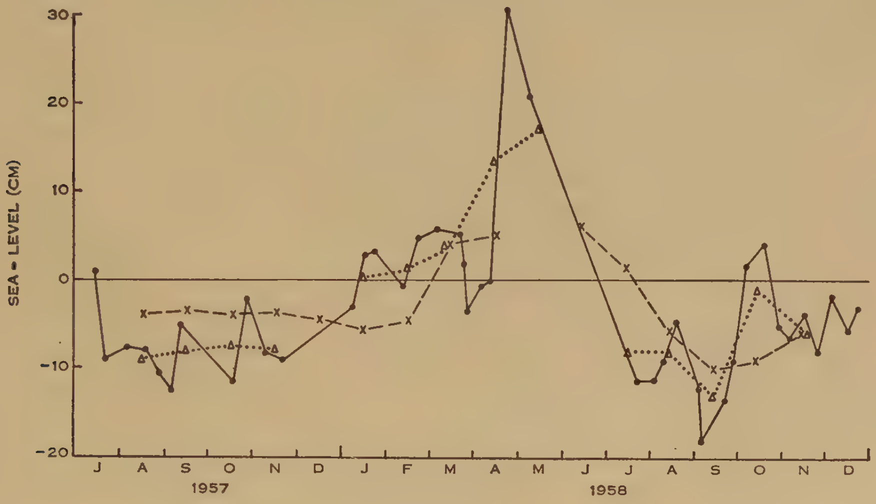

Fig. 4.—Steric and observed sea-levels at Eden.

●———● Steric sea-levels, relative to 500 m, from density observations at 24 mile station.

△······△ Monthly mean of steric sea-levels.

×———× Observed sea-levels, adjusted for variations in atmospheric pressure.

V. Salinity and Temperature Observations

Temperatures and salinities of sea-water were measured at the stations listed in Table 1. The most detailed series of measurements was at Eden, where a hydrographic section was worked at weekly intervals during most of the International Geophysical Year period. This was part of a study of the hydrology of the area in connection with investigations of tuna. Temperatures were measured with reversing thermometers at several depths from the surface to within a few metres of the bottom, and at distances of 4, 8, 12, 16, 20, and 24 miles offshore; water samples were brought up from each depth for laboratory measurements of salinity. The maximum sampling depth at the 24 mile station was 500 m. The same method was used for the measurements at Maria Island, Port Hacking, and Coff's Harbour. The Rottnest Island and Port Moresby temperature and salinity measurements were made *in situ* using a portable temperature–chlorinity bridge (Hamon 1956). The original temperature and salinity data for the stations in Table 1 will appear in C.S.I.R.O. *Oceanographical Station Lists*.

VI. Comparison of Density Changes with Sea-Level Variations

Densities were calculated from the temperature and salinity readings at the Maria Island, Rottnest Island, Eden, Camp Cove, Coff's Harbour, and Port Moresby stations and the changes in sea-level to be expected as a result of the density changes ("steric" sea-level changes) were calculated. Since density changes almost certainly extend to depths greater than the maximum depth of measurement at all stations except Eden, the calculated changes in steric sea-level probably underestimate the actual changes; however, there is no reliable method of extrapolating the density to greater depths.

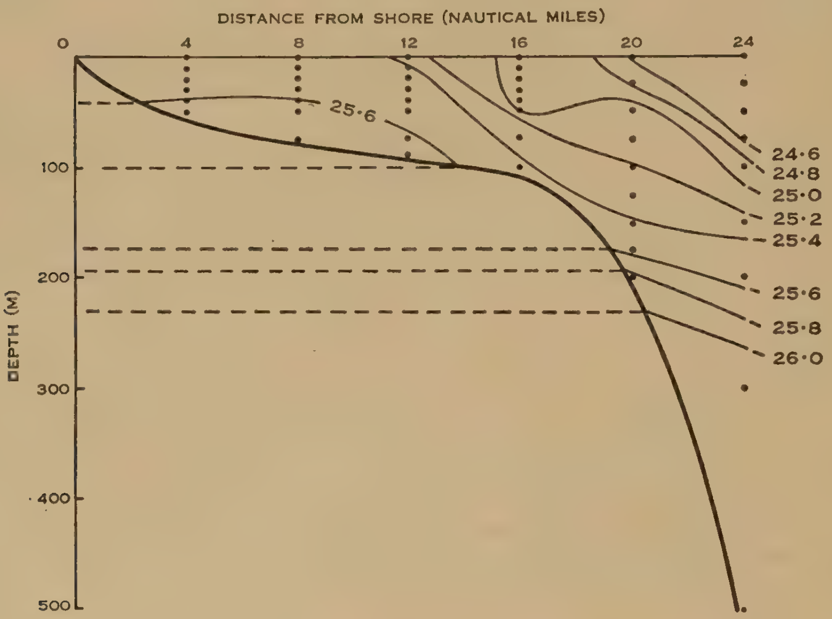

Fig. 5.—Vertical density section off Eden on 22.iv.58. The density contours are in units of σ_t.

(a) Eden

Steric sea-levels at the 24 mile station off Eden were computed from the mean density of the water column between 0 and 500 m and are shown by the continuous line in Figure 4. Monthly means were estimated and are shown by the dotted line, and the adjusted monthly mean sea-levels are shown by the dashed line. This figure indicates that there is little correspondence in detail, although the period of high sea-level from March to June 1958 does coincide roughly with the period of highest steric sea-level. The amplitude of the steric sea-level changes is appreciably greater than that of the adjusted mean sea-levels. This is in general agreement with the results of an earlier study of the relation between observed and steric sea-levels, calculated from measurements to 600 m, off Sydney (Hamon 1957, Figs. 6 and 8).

In comparing the steric and observed sea-levels in Figure 4, it has been assumed that the slope of the sea surface between the coast and the 24 mile station can be neglected. The effects of surface slope have been estimated from the density data at intermediate stations. Vertical sections were plotted, and contours of equal density drawn as in Figure 5. The profile of the sea surface relative to a horizontal surface at a given depth is usually computed from the average density above this depth, assuming that an isobaric surface at the given depth is horizontal. This calculation was extended into shallow water by Helland-Hansen's method (Sverdrup, Johnson, and Fleming 1942, p. 450), in which the contours of equal density are continued horizontally from the points where they intersect the bottom, as shown by the dashed lines in Figure 5. The effective density profile at the 4 mile station was computed in this way for each complete section during the International Geophysical Year period and used to determine the changes in the effective steric sea-level at the 4 mile station relative to a depth of 500 m. The variations in steric sea-level calculated in this way are shown in Figure 6. The differences between Figures 6 and 4 are small, and allowance for the slope of the sea surface near the coast has not materially improved the correlation between steric and observed sea-levels.

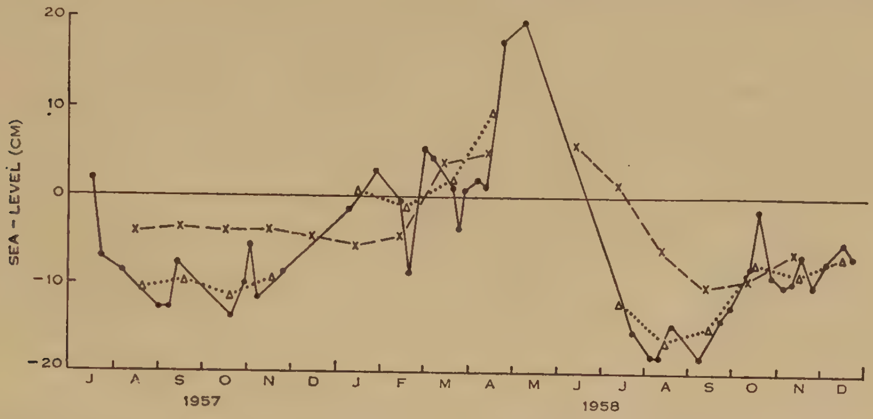

Fig. 6.—Steric and observed sea-levels at Eden, with allowance for slope of the sea surface between the 4 mile and 24 mile station.

●———● Steric sea-levels, relative to 500 m (see text).
△· · · · · ·△ Monthly mean of steric sea-levels.
×———× Observed sea-levels, adjusted for variations in atmospheric pressure.

A remarkable feature of the steric sea-levels at the Eden 24 mile station is the rise of over 30 cm between April 10 and 22, 1958. Calculation of daily sea-levels at intervals of 3 days from April 4 to 22, 1958 showed, however, that no comparable increase in observed sea-level occurred in this period. A more detailed study of daily sea-levels at several east coast ports is in progress.

(*b*) *Rottnest Island, Maria Island, Port Hacking, Coff's Harbour, and Port Moresby*

Comparison of the steric sea-levels at Rottnest Island, Maria Island, Port Hacking, Coff's Harbour, and Port Moresby with the sea-levels observed at the nearest tide gauge stations (see Table 1) is shown in Figure 7. There is a reasonable correlation between observed and steric sea-levels at Port Moresby and Rottnest

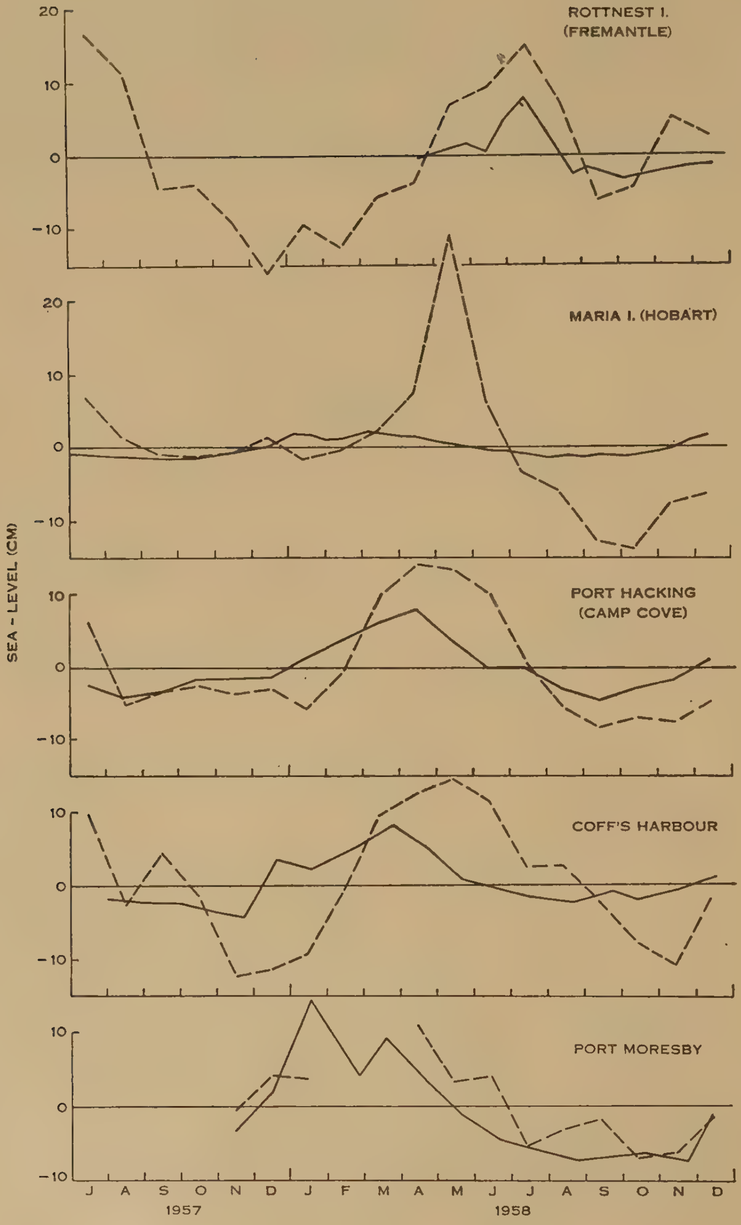

Fig. 7.—Steric and observed sea-levels at Rottnest Island (Fremantle), Maria Island (Hobart), Port Hacking (Camp Cove), Coff's Harbour, and Port Moresby.

—— Steric sea-levels, relative to the maximum sampling depth given in Table 1.

— — — Observed sea-levels adjusted for variation in atmospheric pressure.

Island. The high steric sea-levels from January to April at Port Moresby and June to July at Rottnest Island were due to low salinities, coinciding as expected with the wettest months. At Maria Island, Camp Cove, and Coff's Harbour the variations in steric sea-level are small and the maxima precede the maxima in observed sea-level. Both these facts suggest appreciable density changes at depths below 100 m, which, if included, might give better coincidence between the pairs of curves of Figure 7.

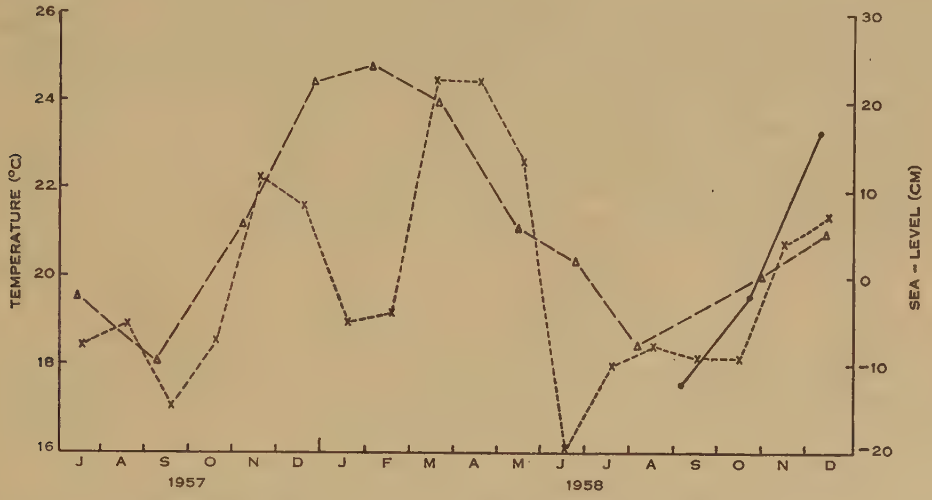

Fig. 8.—Sea-levels, surface temperatures, and steric levels at Lord Howe Island.
× – – – × Sea-levels adjusted for variations in atmospheric pressure.
△ — —△ Sea surface temperatures.
●————● Steric sea-levels, relative to 1000 m.

Since the sea-levels at Hobart may be influenced by river discharge (Section IV) the Maria Island steric levels have been compared also with Maatsuyker Island sea-levels, but the correlation is no better than with the Hobart sea-levels.

(*c*) *Lord Howe Island*

Surface temperatures were obtained by M.V. *Tulagi* near Lord Howe Island at intervals of about 6 weeks. Only a qualitative comparison of surface temperature with sea-level (Fig. 8) is possible in this case. Three times towards the end of 1958 F.R.V. *Derwent Hunter* occupied a station to 1000 m depth near the island. The steric sea-levels relative to 1000 m have also been entered on Figure 8. There is general agreement between the steric and observed sea-levels, although, as at Eden, the changes in steric level are somewhat greater than the observed sea-level changes.

VII. Discussion

The observations at Eden are of special interest, since they show that steric sea-level changes relative to 500 m in the immediate vicinity of the tide gauge are not reflected in detail in the sea-levels observed at the tide gauge, although there is general agreement on a seasonal basis. It appears that seasonal variations in sea-level are largely due to variations in sea-water density as required by the isostatic hypothesis, but that short-term variations in sea-level may not be isostatic.

The large sea-level changes at Lord Howe Island are probably connected with variations in the position of the East Australian Current. Dynamic calculations (C.S.I.R.O. Aust. 1958, 1959*a*, 1959*b*, 1960*a*, 1960*b*) have shown that this current often turns away from the coast a little north of Sydney, and then turns north-eastwards towards Lord Howe Island. If this flow continues as far as Lord Howe Island but varies in position (owing, for example, to meanders of the kind found in the Gulf Stream after it leaves the American continental slopes) one would expect large variations in steric sea-level at Lord Howe Island, and also that these would not correlate well with variations at mainland stations.

If allowance is made for the shallowness of sampling at many of the stations where steric observations were made, it may be concluded that the results reported in this paper conform generally with the isostatic hypothesis.

VIII. ACKNOWLEDGMENTS

The tide gauges and salinity–temperature meters at Maatsuyker Island, Cape Sorell, Port Moresby, and Rottnest Island were provided out of the Commonwealth Government International Geophysical Year grant to the Universities. We desire to acknowledge the help which has been extended to us by many people in the course of this work. Professor J. C. Jaeger was responsible for organizing the Universities' programme in oceanography and Sir Guy Wyatt gave particular assistance with the stations at Cape Sorell and Maatsuyker Island. Commander C. G. Little installed and operated the tide gauge and made the steric sea-level measurements at Port Moresby; Dr. E. P. Hodgkin obtained the records at Rottnest Island, Captain MacLean those at Cape Sorell, and officers of the Lighthouse and Navigation Service those at Maatsuyker Island. Sea-level data at ports with established tide gauges were made available by the officers responsible for the gauges in each State.

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AREA OF DISTRIBUTION, AND MOVEMENT OF THE WESTERN SUBSPECIES OF THE AUSTRALIAN "SALMON", *ARRIPIS TRUTTA ESPER* WHITLEY*

By W. B. Malcolm†

[*Manuscript received August* 22, 1960]

Summary

Evidence provided by the commercial fishery, tagging operation, and direct observation of the schools is used to give a general account of the area of distribution and movements of this subspecies. A study of some aspects of the reproductive cycle has furnished evidence on the location of the spawning area. Some age data are used, but conclusions regarding age are exceedingly tentative and are not essential to the general account. The implications of this account with regard to the total area of distribution and the magnitude of the entire stock are discussed.

I. Introduction

The Australian "salmon", *Arripis trutta* (Bloch & Schneider), is a marine pelagic species endemic to the waters of the Australian–New Zealand region. Although it has long been known that the species occurs in large numbers along the southern coast of Australia, with the exception of Victoria where salmon was accepted by the fresh fish market no real demand existed for the fish. The absence of demand precluded the early development of intensive fisheries in other areas but, with the discovery of a satisfactory canning technique and the establishment of a series of canneries, active fisheries developed in New South Wales, Western Australia and, to some extent, South Australia, between 1936 and 1949.

The development of the New South Wales and Western Australian fisheries stimulated a scientific investigation of the species, and it became evident that several breeding communities of salmon exist. Fairbridge (1950) suggested that the New Zealand and Lord Howe Island stocks probably constitute separate breeding communities; he also provided evidence to show that there were two well-defined groups, which he designated as subspecies, occurring on the southern coast of Australia. The morphology of these subspecies has been further discussed (Malcolm 1959). The western subspecies has been shown to occupy Western and South Australia and to be the predominant form in western Victoria and the more westerly regions of Tasmania, while the eastern subspecies occupies New South Wales and is the predominant form in the more easterly regions of Victoria and Tasmania. Both subspecies occur together in schools in many areas in Victoria and Tasmania. Whitley (1951) designated the western subspecies as *Arripis trutta esper* Whitley and the eastern subspecies as *Arripis trutta marginata* Cuv. & Val.; the name *Arripis trutta trutta* has been reserved by Whitley for the New Zealand stock.

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* Part of a thesis submitted for the degree of Doctor of Philosophy, University of Western Australia.

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This paper discusses the distribution of the western subspecies adults and juveniles, the location of the spawning ground from evidence provided by a study of the reproductive cycle, the migration of the maturing fish from the area of juvenile distribution to that occupied by the adults, the seasonal migration of the adults, and the movement of the early life-history phases to the nursery areas.

II. DISTRIBUTION

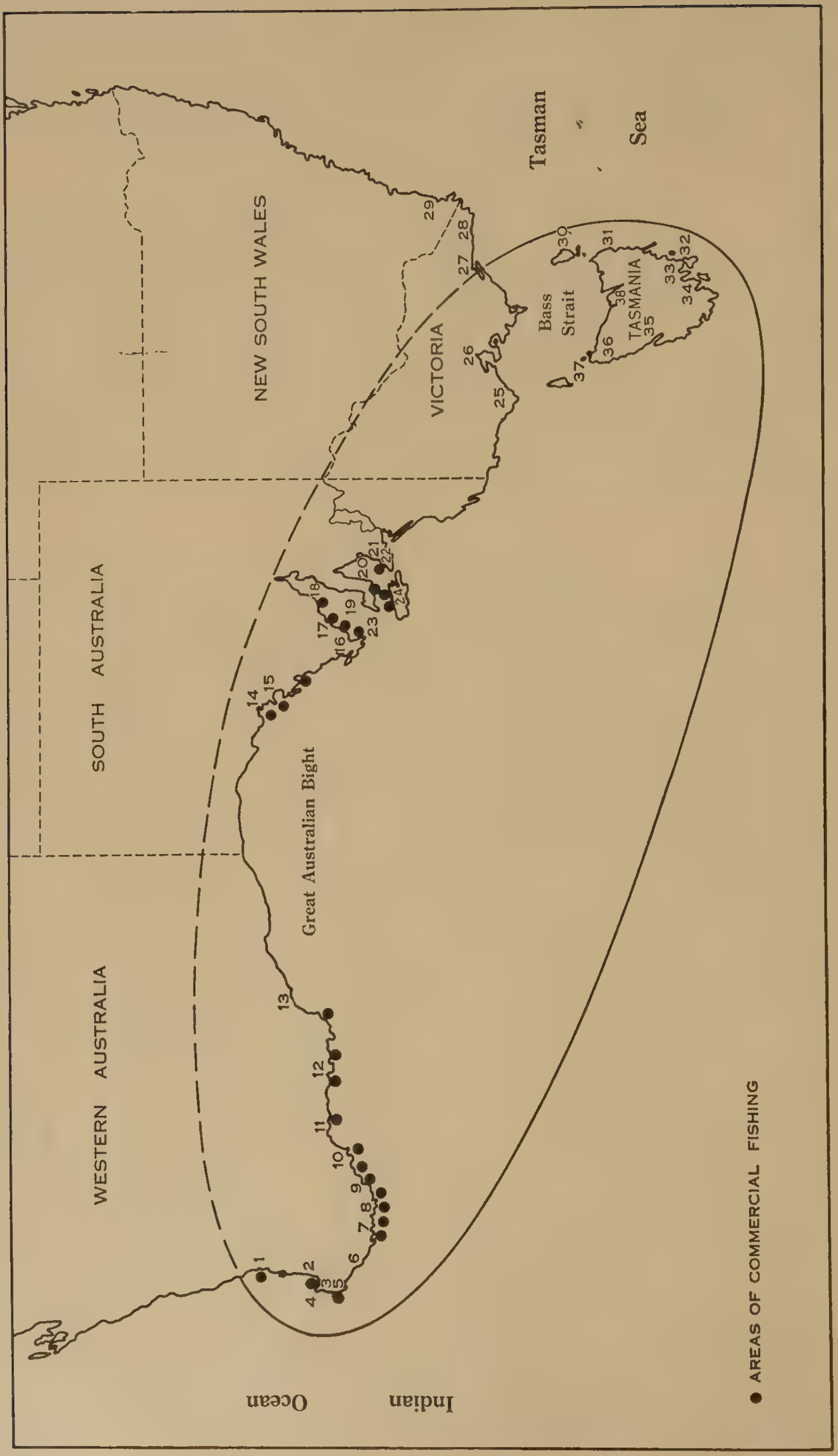
The salmon has an inshore schooling habit as a result of which large schools appear in the shallow water on the beaches or adjacent to reefs or headlands (Plate 1); the fishery is conducted by beach seine and is concentrated on these inshore schools. Abundant observations on inshore occurrences have been made from vantage points on the shore or from the air, but the schools have been seen away from the coast only comparatively rarely. There are reasons for believing that the fish does spend some of its time in deeper water, but the evidence of this is relatively scant as is understandable both from the behaviour of the fish and from the nature of opportunities for observation in the area of its distribution (Section II(*b*)).

(*a*) *Coastal Occurrences*

In Western Australia the schools occur regularly in the inshore waters between the Perth area and Point Culver. The commercial fishery operates between these localities (Fig. 1), and the coastline is under the continual surveillance of beach observers and a cannery spotting plane. The Perth area may be taken as the northerly limit of the distribution on the west coast because salmon are not captured in the more northern regions; there are various fishing operations in these regions and the fishermen would take salmon if they occurred there. The relative paucity of records of salmon between Point Culver and Ceduna is to be taken as indicative of the possibilities of and opportunities for observation rather than as evidence on the density of salmon stocks in these areas. The coastline is sparsely populated and many of the beaches are inaccessible; moreover, aerial observation is difficult because much of the coastline comprises steep cliffs rising from deep water whereas salmon schools are observed most easily from the air when they are frequenting the shallow surf zone on the beaches. The presence of the salmon in the area between Point Culver and Ceduna is established by captures made by the few local residents and visitors angling for the species, and in any case must occur because the area is traversed by migrating fish (Section IV(*a*)).

East of Ceduna the subspecies is abundant in South Australian waters and occurs in Victorian and Tasmanian waters where, in many areas, it has been found mixed in schools with the eastern subspecies. In Victoria, only the western subspecies is found in the more westerly areas, and is the predominant form in the Port Phillip Bay region. The eastern form is the predominant form east of Port Phillip Bay, although the western form is relatively common as far east as Lakes Entrance, and has been recorded at Eden in New South Wales.

In Tasmania it is possible that both subspecies occur in all areas. The general impression gained from the samples that have been handled is that the west coast is occupied chiefly by the western subspecies whereas the north-eastern area is


WESTERN AUSTRALIA
SOUTH AUSTRALIA
NEW SOUTH WALES
VICTORIA
TASMANIA
Great Australian Bight
Bass Strait
Tasman Sea
Indian Ocean
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3
4
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● AREAS OF COMMERCIAL FISHING

Fig. 1.—Map of southern Australia, showing distribution of western subspecies, areas of commercial fishing, and localities mentioned in text. (For meaning of numerals see opposite page.)

occupied chiefly by the eastern subspecies. The northern and the south-eastern coasts are mixing areas, but the western subspecies is the predominant form on the northern coast at least as far east as Port Sorell, and on the south-eastern coast at least as far north as Dunalley (Table 1).

TABLE 1

PERCENTAGES OF EASTERN AND WESTERN SUBSPECIES IN SAMPLES OF SALMON EXAMINED IN TASMANIA

Locality	Total No. of Fish	Eastern Subspecies		Western Subspecies	
		No.	Percentage of Total	No.	Percentage of Total
St. Helens	36	30	83	6	17
Dunalley	24	6	25	18	75
Gordon	19		0	19	100
Dover	174	41	24	133	76
Macquarie Harbour	3		0	3	100
Arthur River	13		0	13	100
Stanley	18	2	11	16	89
Port Sorell	173	43	25	130	75

(b) *Seaward Occurrences*

Since there is no evidence to suggest that the western subspecies differs from the eastern subspecies with regard to its seaward occurrences, data for the two subspecies are used collectively in this discussion.

Whilst it is generally believed that the Australian salmon is an onshore pelagic species, there are various pieces of evidence to show that it spends some of its life in deeper water, even if only little is known of its seaward distribution. The overwhelming bulk of evidence on the presence of the schools in the shallow water zone

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Fig. 1 (*continued*)

1 Perth
Safety Bay
2 Bunbury
3 Busselton
Eagle Bay
Meelup
4 Smith's Beach
5 Cape Leeuwin
Hamelin Bay
Augusta
6 Chatham I.
Nornalup
7 Peaceful Bay
Boat Harbour
Parry's Inlet
Denmark
8 Albany
Torbay
Two People Bay
Nanarup Beach
9 Cheyne Beach
Cape Riche
10 Bremer Bay
Doubtful I.
Dillon Bay
11 Hopetoun
12 Esperance
13 Point Culver
14 Ceduna
15 Streaky Bay
16 Port Lincoln
Tumby Bay
17 Port Neill
18 Cowell
Whyalla
Port Pirie
19 Spencer Gulf
20 St. Vincent Gulf
21 Adelaide
22 Port Noarlunga
Rapid Bay
23 Wedge I.
24 Kangaroo I.
25 Lorne
26 Port Phillip Bay
Melbourne
27 Lakes Entrance
28 Mallacoota
29 Eden
Merimbula
30 Babel I.
31 St. Helens
32 Dunalley
Triabunna
33 Hobart
34 Dover
Partridge I.
Gordon
35 Macquarie Harbour
36 Arthur R.
37 Stanley
Hunter I.
38 Port Sorell

along the coast led Blackburn and Tubb (1950) to suggest that the large proportion of the Australian salmon population occurs in the narrow band of water within a mile or two of the shore.

The evidence of seaward distribution may be summarized as follows:

(1) Reports, most of them unconfirmed, indicate that salmon schools occur throughout continental shelf waters and even in oceanic areas. Fairbridge (1950) states that shoals are not commonly sighted beyond the continental shelf, but that there are reports, apparently reliable, of salmon shoals being sighted, and specimens being caught, well out in the Tasman Sea. Unconfirmed reports have been made of the presence of salmon schools towards the edge of the continental shelf in the Great Australian Bight.

(2) Tagging studies show that both subspecies cross Bass Strait in migration from Tasmania to Victoria and New South Wales (Section IV(*b*)).

(3) The predominant diet of the subspecies indicates that feeding takes place away from the beaches. The eastern subspecies is a plankton feeder, the euphausiid *Nyctiphanes australis* Sars comprising the major part of the diet, while the western subspecies has as its main diet the pilchard, *Sardinops neopilchardus* (Steindachner). Tagging studies conducted in Western Australia during the non-spawning phase indicate an inshore–offshore movement, presumably related to feeding (Section IV(*c*)).

(4) Marked fluctuations in the number of schools in the shallow water along the coast can only be explained if the inshore schools represent only a proportion of the total population.

The absence of regular reports of seaward occurrences need not preclude any suggestion of a general distribution over the entire shelf area. In most areas throughout the range, little fishing of any nature takes place outside the immediate inshore zone, and it is probable that while at sea the schools rarely appear on the surface. In the shallow water zone, the schools remain below the surface normally and are detected because their colour contrasts with the sandy bottom rather than because they ruffle the surface. Once beyond the shallow water zone the schools would no longer be visible.

(*c*) *Differential Distribution of the Adults and Juveniles*

Length-frequency measurements are available for the commercial catches in Western Australia, South Australia, Tasmania, and Victoria. In Western Australia over 10,000 measurements were collected between 1949 and 1955, in South Australia over 6000 between 1952 and 1955, in Tasmania approximately 6000 between 1939 and 1952, and in Victoria approximately 50,000 between 1939 and 1946.

In Western Australia, the lengths of the salmon taken by the beach fishery operating between Perth and Hopetoun fall into a single modal group between 52 and 80 cm (Fig. 2). This fishery does not capture smaller fish. In 1948 and 1949, large quantities of salmon were present on the beaches east of Esperance, and commercial fishing indicated a more diverse size range that that normally taken between Hopetoun and Perth. Although the usual large fish were present, considerable quantities of a small size group, between 40 and 50 cm (Fig. 2), were captured.

The presence of this small size group in the Western Australian beach catch must be regarded as atypical since the fish did not reappear in the Esperance area in later years. Although the mesh size of the beach seines used in Western Australia is large to allow the use of longer nets with a minimum of manpower, the particular mesh size used has been selected because it is most suitable to take the fish in the schools. Since the schools are clearly visible from the shore, any large and regular escape of fish of smaller size would be observed and smaller mesh seines would be brought into use. The use of smaller mesh is permissible and the capture of smaller fish is allowed by law (the legal minimum length is 22 cm); small fish are accepted by the canneries and the fresh fish market.

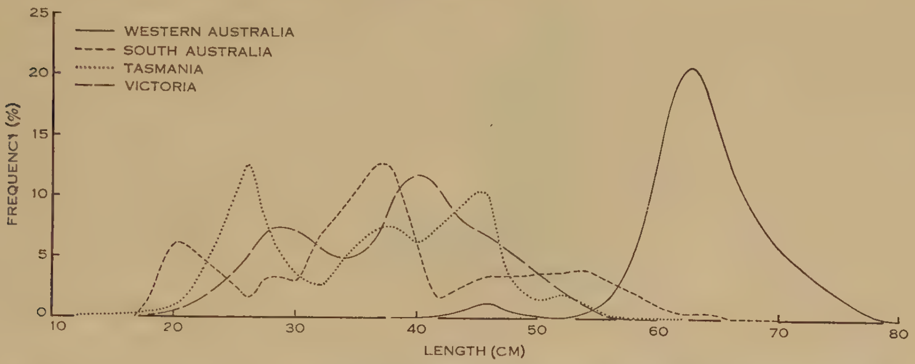

Fig. 2.—Length frequency distribution of the Australian salmon taken by the commercial fisheries in Western Australia, South Australia, Tasmania, and Victoria. The Western Australian and South Australian catches comprise the western subspecies, while the Tasmanian and Victorian catches comprise both eastern and western forms.

Small fish, from 25 to 35 cm, are taken occasionally in the estuaries between Perth and Albany. The annual catch of these fish would be less than 5 tons, and apart from this there are no regular catches of small salmon in Western Australia. Such small numbers of young fish could not provide the recruitment required for a population providing an annual catch of between 1300 and 2800 tons. Obviously recruit stocks must be located in areas other than those fished by Western Australian fishermen.

No commercial fishing or other sampling has been carried out between Esperance and Ceduna, but from Ceduna eastwards throughout South Australia the fishery operates mainly on size groups smaller than those normally taken by the beach fishery of Western Australia (Fig. 2); the commercial catch in South Australia from 1952 to 1955 comprised fish between 18 and 70 cm. Although the larger fish of South Australia are of about the same size as those taken normally in Western Australia, these larger fish are only a small percentage of the South Australian catch. Approximately 85 per cent. of the fish in the South Australian catch are less than 52 cm, which is the length of the smallest fish taken by the regular Western Australian beach fishery.

The South Australian catch consists of two general size groups. The fish taken in the bays, in Spencer and St. Vincent Gulfs, and on the coastal flats are generally of small size (20–40 cm), while those taken on the open beaches, particularly around Kangaroo Island and other coastal islands, are generally of larger size (40–70 cm). Since most South Australian fishing takes place in the bays and on sheltered beaches, which is the habitat of the modal group between 30 and 40 cm long, it is natural that this group should dominate the catches, but there are grounds for believing that the composition of the stock is other than that indicated by the catch. The open beaches, for example, especially along the shores of Kangaroo Island, are inhabited by fish of length from 40 to 70 cm whose relative abundance is not accurately shown by the catch composition. However, although the picture of this population given by the data so far collected in this study is certainly incorrect as to the relative abundance of the large fish, it correctly shows that the young fish, missing from the Western Australian catches, are to be found in South Australian waters in numbers such as to suggest that a main if not the principal nursery area lies in these waters. This interpretation of the evidence must be modified to accommodate evidence from Tasmania and Victoria where fish of this subspecies are taken in the commercial catches. The composition of these catches of salmon, comprising both subspecies, is represented in Figure 2; although in the course of the measuring of these salmon it was impossible to differentiate the fish into their subspecific groups, the meaning of the picture is clear: the majority of the Tasmanian and Victorian fish lie in the range 20–50 cm, corresponding to the

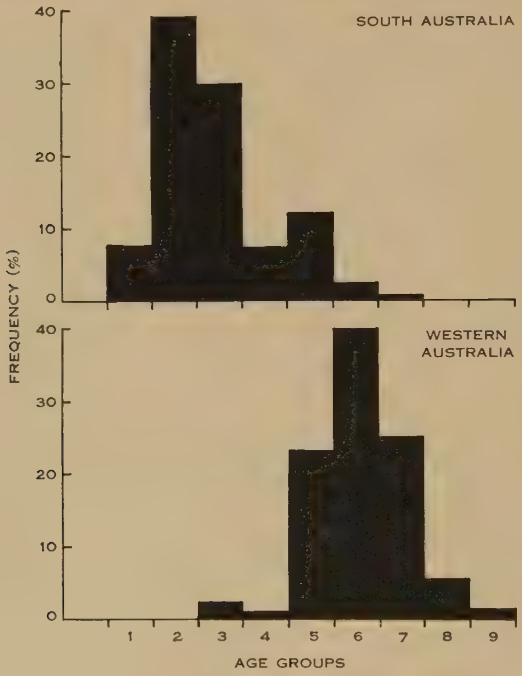

Fig. 3.—Age composition of the Western Australian and South Australian commercial catches of Australian salmon.

range to which the majority of South Australian fish belong. Hence it is clear that the area inhabited by the small fish of the western subspecies includes Tasmanian and Victorian waters.

The Western and South Australian length-frequency data have been converted into age groups (Fig. 3). For each length interval, the individual age was determined on a number of fish. The number of fish in each age group within the length interval was then expressed as a percentage of the number of that interval. These percentages were then applied to the number of fish in a much larger sample for which length measurements had been taken. In this way a table was constructed showing the number of fish of each age group in each length interval. The total frequency in this table was as much as 20 times greater than the number on which age had been determined. The application of this method to length frequency data resulted in the preparation of Figure 3 using the lengths of some 16,000 fish.

The distribution of "0" group fish, ranging from 5 to 12 cm in length, as shown by netting with a small mesh beach seine, shows a marked similarity to the distribution of the larger juveniles. In Western Australia the group is virtually absent from the area between Perth and Hopetoun, but in 1949 was abundant on the beaches in the Esperance area; sampling in this area was not possible in other years. No data were collected for the area between Esperance and Ceduna, but the group is abundant throughout South Australia and Victoria as far east as the Port Phillip Bay region. Between Port Phillip Bay and Lakes Entrance reasonable quantities were netted. In Tasmania, the western subspecies "0" group is abundant in the westerly areas on the north coast, and the southerly areas of the east coast; fishermen operating on the west coast report an abundance of the group.

III. Reproduction

As the eggs and larvae of the Australian salmon are unknown, it has not been possible to delineate the spawning area of the western subspecies from evidence of the distribution of the eggs and early larvae in the plankton. Moreover, the small number of plankton collections made in the area from Western Australia to Tasmania would afford only a scant basis for such a study. As an alternate approach an attempt has been made to delimit the spawning area by deductions that may be drawn from a detailed study of the reproductive cycle. Monthly gonad samples were obtained from both Western Australia and South Australia, but no material was collected for Victoria or Tasmania. Testis and ovarian tissue was sectioned and stained with haematoxylin and eosin, while counts and measurements of ova were made on formalin preserved material.

(a) *The Ovarian Cycle*

The most rapid and satisfactory analysis of the ovarian cycle was made by means of ova-diameter measurements on material preserved in 10 per cent. formalin. Samples of 50–100 ovaries from both South Australia and Western Australia were examined each month. The method of counting employed by Orcutt (1950) proved the most convenient. The ovarian tissue was teased out on a microscope slide and the diameters of the few largest ova measured under a microscope equipped with a micrometer eyepiece. The mean diameter of these large ova was then determined; the various mean values obtained in each monthly sample are shown in Figure 4. Obviously distorted ova were not measured. Full ova-diameter counts using the method of Clark (1934) were made on selected material (Fig. 5).

The data for the Western Australian and South Australian ovarian cycles are summarized in Table 2. The ovarian cycle in Western Australia can be divided into two phases, a non-spawning phase or period of relative quiescence, and a spawning phase or period of marked activity. The non-spawning phase, July to January, is characterized by the presence in the ovary of only primary oocytes. The maximum diameters of the primary oocytes are less than 0·2 mm (Figs. 4 and 5) and their cytoplasm shows a strong affinity for haematoxylin (Plate 2, Fig. 1).

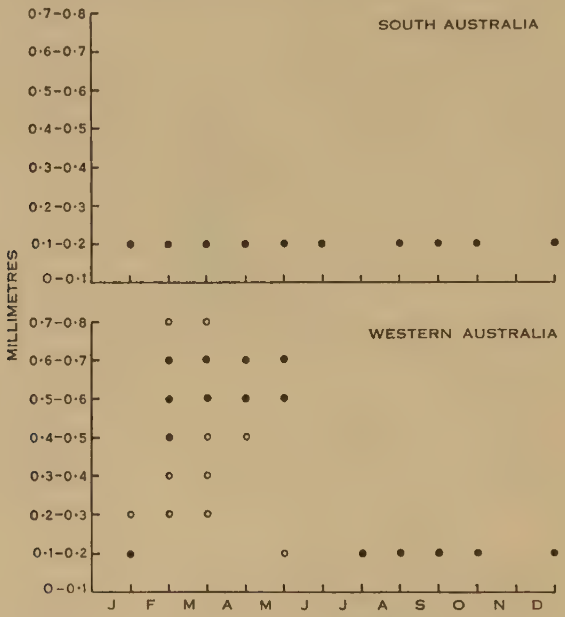

Fig. 4.—Monthly size progression of ova in fish from Western Australia and South Australia. The size of the largest ova found in each ovary in the monthly samples is shown by a circle. A solid circle indicates that a large number of the females carried ova of that size.

The spawning phase, February to June, includes active pre-spawning ovarian development and maturation, and post-spawning degeneration and resorption. The developing ovaries are characterized by the presence of secondary oocytes; these oocytes are between 0·4 and 0·8 mm in diameter (Figs. 4 and 5) and possess yolk which stains deeply with eosin (Plate 2, Fig. 2).

Some indication of the actual spawning period may be obtained from the macroscopic appearance of the ovary, and the presence of degenerating ova in the follicles. In February, March, and early April most of the ovaries are large and taut and contain large numbers of maturing ova. Post-spawning degenerative changes have not been observed in this period. In late April, and particularly in May, although large ova are still present in the follicles, many of these ova have commenced to degenerate (Plate 2, Fig. 3). The ovaries, although still large, are relatively flaccid, and it is apparent that one or more batches of ova have been spawned. In most of the individuals, a few ova may be extruded from the vent upon application of stripping pressure; obviously since these mature ova have not been observed in the follicles they must have remained in the oviduct after spawning. The absence of individuals showing immediate post-spawning degeneration before mid April, and their abundance in the catches in late April and May, suggests that April and May are the months of intense spawning, and that little or no spawning takes place in February and March. It is unlikely that intense spawning takes place in June since the ovaries are completely flaccid and bloodshot, and the follicles show only the remains of degenerating large ova at that time (Plate 2, Fig. 4).

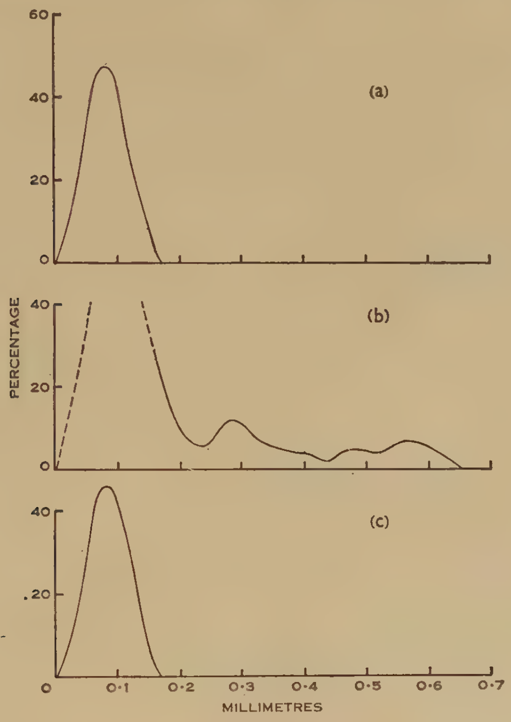

Fig. 5.—Frequency polygons of the diameters of the eggs in the ovary. Typical individuals from (*a*) Western Australia during the non-spawning phase, (*b*) Western Australia during the spawning phase, (*c*) South Australia throughout the year.

Coastal pre-spawning and post-spawning migrations are associated with the spawning phase gonad activity in Western Australia (Section IV(*c*)). Whereas in Western Australia the marked ovarian development and migration are well known to all concerned with the fishery in the area, in South Australia, western Victoria, and the westerly regions of Tasmania no ovarian condition or migratory behaviour that could be indicative of spawning is known to the fishermen or fisheries administrators. There are no reports of the finding in these areas of a large number of fish in which the ovaries showed spawning development, although from time to time reports have been made of the appearance in the catches of an occasional female showing maturing ovaries. Field observations, and monthly ovarian samples

TABLE 2

SUMMARY OF DATA ON SEASONAL OVARIAN ACTIVITY IN WESTERN AND SOUTH AUSTRALIA

Period	Western Australia	South Australia
July to January	No marked activity; ovaries reddish in colour and transform from a complete flaccidness in July to a relative tautness in January. Ova not visible macroscopically. Maximum diameter of the largest ova less than 0·2 mm. Primary oocytes only; cytoplasm shows affinity for haematoxylin	Throughout the year ovaries relatively taut or taut, pinkish or reddish, with no macroscopically visible ova. Maximum diameters of largest ova less than 0·2 mm. Primary oocytes only
February and March	Period of marked ovarian development. Some ovaries still small and reddish in colour, but most show marked increase in size, creamish colour, and macroscopically visible ova. Maximum diameters of largest ova 0·3–0·8 mm, mainly 0·4–0·7. Enlarged ovaries contain yolk bearing secondary oocytes; yolk stains deeply with eosin	
April	In early April all ovaries show enlargement, creamish colour, and macroscopically visible ova (secondary oocytes). Maximum diameters of largest ova 0·4–0·8 mm, mainly 0·5–0·7. In late April, some ovaries show flaccidness	
May	Most ovaries still large and creamish in colour, but relatively flaccid. Maximum diameters of largest ova 0·5–0·7 mm. Large ova invariably show degenerative changes. Some ovaries small, flaccid, and bloodshot; largest intact ova less than 0·2 mm in diameter	
June	Ovaries small, bloodshot, and flaccid. No ova-diameter measurements. Remains of degenerating ova	

taken where possible from fish about the same size (approximately 60 cm) as those captured in Western Australia, show that in South Australia throughout the year the ovaries are immature. The ovaries are small and contain primary oocytes only; the maximum diameters of the primary oocytes are less than 0·2 mm (Figs. 4 and 5).

In the absence of evidence of ovarian development and maturation in South Australian salmon, it is concluded that spawning does not occur in South Australian waters. The ecological and biological evidence available for the western subspecies fish in Victoria and Tasmania allows the belief that no spawning occurs in these areas.

(*b*) *The Testicular Cycle*

Testicular material was fixed in Bouin's fluid and stained with haematoxylin and eosin. An attempt was made to collect monthly samples from both Western and South Australia, but the series for each area is incomplete. However, although it was not possible to follow the process of spermatogenesis throughout the year in either area, sufficient material was collected to allow a comparison of the general testicular cycle of the Western Australian with that of South Australian fish.

No materials for histological examination were collected in Western Australia between August and December; by January active spermatogenic development is evident (Table 3). This development reaches its peak in March and April when the testicular tubules of most fish are occupied fully by spermatozoa (Plate 3, Fig. 1), and milt flows freely from the genital opening when the fish are handled or stripped. It is evident that many of the fish taken in the commercial catches in May have accomplished spawning because the testes are relatively flaccid; in some of these fish milt no longer flows freely from the genital opening with stripping, but exudes from the cut surface of the testis when pressure is applied to the organ. Active post-spawning degeneration is completed by July since the testicular tubules are lined with primary germ cells in that month.

The presence of spermatozoa in the testicular tubules is not in itself an indicator of the spawning period in Western Australia. Spermatozoa are found as early as January, and since no material was collected between July and December it is impossible to put a precise date on their first appearance but it is possible that they have been formed well before December. However, since running ripe males are not encountered before the end of February, and the July catches are dominated by fish showing post-spawning recovery, it is evident from the testicular development that spawning is accomplished between March and June; this is in conformity with the conclusion, reported above with respect to females, that April and May are the principal months of spawning.

Spermatogenesis is completed in the larger males (above 50 cm) in South Australia, and the spermatogenic cycle in the South Australian fish appears to follow in time the Western Australian cycle. No material was collected in South Australia between May and July, but in August the testicular tubules are lined with primary germ cells and occasional cysts of spermatogonia are present (Table 3).

TABLE 3

SUMMARY OF DATA ON SEASONAL TESTICULAR ACTIVITY IN LARGE FISH (ABOVE 500 MM) IN WESTERN AND SOUTH AUSTRALIA

Period	Western Australia	South Australia
July	Testes small and taut. Blood extruded from lumen when testis cut and pressure applied. Tubules lined with primary germ cells	
August and September	Testes small and taut	Testes small and taut. Blood exudes from lumen when testis cut and pressure applied. Tubules lined with primary germ cells. Occasional cysts of spermatogonia
November and December		Testes small and taut. Majority of tubules lined with primary germ cells, but in some all stages of spermatogenic development from spermatogonia to spermatozoa
January	Slight enlargement of testes. Milt extruded from cut surface of testis when pressure applied. Active spermatogenesis, all stages from spermatogonia to spermatozoa in tubules	Testes small and taut. Milt extruded from cut surface of testis when pressure applied. Active spermatogenesis, all stages from spermatogonia to spermatozoa in tubules
February	Marked enlargement of testes in many fish with milt extruded from the genital opening with stripping. All phases of spermatogenic development in the tubules	Some enlargement of the testes. Milt extruded from cut surface of testis when pressure applied. Active spermatogenesis, all phases of development in the tubules
March	Testes large and whitish in colour. Milt flows freely from the genital opening when fish handled or stripped. All spermatogenic phases in tubules of some fish, in others tubules contain spermatozoa only	
April		Decrease in size of testes. Spermagenic products in tubules in process of degeneration
May	In many fish testes still large and taut with milt flowing freely from genital opening with stripping. In other fish, testes large but relatively flaccid; milt not extruded from genital opening with stripping, but exudes from cut surface of testis when pressure applied. Mainly spermatozoa in tubules	

Spermatozoa are observed in some tubules as early as December, and spermatogenesis is particularly marked in January and February. In February, some tubules contain only spermatozoa, while the remainder are occupied by all stages of spermatogenic development (Plate 3, Fig. 2). No material was collected in March, but by April active degeneration of the spermatogenic products in the tubules is evident (Plate 3, Fig. 3).

It was concluded above that since oogenesis past the primary growth phase of the primary oocytes was not observed in fish from South Australia, spawning does not take place in South Australian waters. Thus, even although spermatogenesis is completed in the larger males, reproduction could not take place. At the height of spermatogenesis in the South Australian males, if the testis is cut and pressure applied to the organ, milt exudes from the cut surface. However, the testes show little enlargement, milt is not extruded from the genital opening with stripping pressure, and there is no evidence to suggest that spermatozoa are shed by the South Australian fish. It therefore appears as if complete resorption of these products must take place.

Testicular material was not collected for western Victoria or the more westerly regions of Tasmania. Although there are no reports of running ripe males having been encountered in these areas, it is possible that spermatogenesis is completed in the larger males here as happens in South Australia.

(*c*) *Location of the Spawning Area*

It was concluded above, on the evidence of ovarian development, that spawning does not occur in South Australian waters, and it was considered that this conclusion was applicable also to the waters of western Victoria and the more westerly regions of Tasmania. The seasonal development of the ovaries and testes of the Western Australian fish is an obvious phenomenon, and it is evident that spawning takes place in Western Australian waters. Although the delineation of the spawning area must await a detailed study of the distribution and abundance of recently spawned eggs, seasonal distribution, migration, and gonad condition do provide indirect evidence which must be examined.

In Western Australia, the distribution of the large fish extends from Perth to the Esperance area, and possibly even further into the Great Australian Bight, with salmon concentrated in the Hopetoun and Esperance areas only during the period from July to January (Section IV(*c*)). The period from July to January is the period of quiescent gonad activity or non-spawning phase. Between February and June, the spawning phase, few fish are encountered in the Hopetoun and Esperance areas, and it is not conceivable that these areas are regions of intensive spawning.

In the spawning phase, the population is concentrated in the area between Bremer Bay and Busselton, but it is believed that the region of intensive spawning is centred in the Busselton–Cape Leeuwin area. This area represents the apparent end-point of the pre-spawning movement (Section IV(*c*)), and is the only area in which any concentration of fish is observed in late April and May; it was suggested above that April and May are the months of intensive spawning. Moreover, the only fish observed with gonads in immediate post-spawning condition are those taken on the beaches between Cape Leeuwin and Busselton, which suggests that these beaches are in close proximity to the spawning area.

In the area between Bremer Bay and Parry's Inlet, large schools of salmon are observed and netted during the spawning phase, but it is doubtful that intensive spawning occurs in this area since the schools appear to be more or less continually on the move. From late February to mid April, the schools move in a westerly direction towards the Busselton area (Section IV(*c*)), and the fish have large and developing gonads. Few fish are observed between Parry's Inlet and Bremer Bay in late April and in May, but in June, and to some extent July, schools are relatively abundant; the gonads are in an advanced state of degeneration and resorption, and the fish move in an easterly direction.

Since few ripe females have been recorded during the course of the investigations in Western Australia, and no behaviour of the inshore schools that could be interpreted as spawning has been observed, the conclusion that spawning takes place at sea seems warranted. If this conclusion can be accepted, the absence of the schools from the beaches between Parry's Inlet and Bremer Bay in late April and May can then be explained as a result of the fish moving away at that time to spawn. Some spawning may well occur in the area, but as the fish are abundant in the Cape Leeuwin–Busselton region in late April and May, and fish in immediate post-spawning condition normally are not encountered in the area between Bremer Bay and Parry's Inlet, it is possible that the schools observed in this area between February and mid April continue their movement to the Cape Leeuwin–Busselton area before spawning takes place. This westerly pre-spawning movement has been confirmed by tagging operation (Section IV(*c*)).

In some years schools of salmon appear in the Perth area but, like the Hopetoun and Esperance occurrences, the appearance of schools in the Perth area is confined to the non-spawning phase. A portion of the population may disperse northwards after spawning to spend some time in the Perth area before returning to southern waters (Section IV(*c*)).

The evidence concerning the location of the spawning area is limited and indirect, but it does seem to indicate that although some spawning may occur throughout the entire area of the adult distribution, the region of intensive spawning is extremely small in relation to the overall distribution of the subspecies, and that it is centred in the area between Cape Leeuwin and Busselton.

IV. MIGRATION

It was concluded in the preceding section that spawning is confined to Western Australia, and evidence is presented leading to the view that intense spawning takes place in the area between Busselton and Cape Leeuwin. South Australia, western Victoria, and the more westerly regions of Tasmania are held to be the nursery areas, on the evidence that smaller fish are taken in these areas and are not taken other than in very small quantities in Western Australia. If the foregoing is true, movement of young stages eastwards from Western Australia must take place, and conversely juvenile but maturing fish must migrate to Western Australia for spawning. No attempt has been made to study the eastward movement, but efforts have been directed toward confirming the details of the general distributional picture already formed, by analysing the movements of juveniles and adults that serve to maintain this picture. Much of the evidence on which this study is based comes from analysis of commercial catches and of reports of observations. This evidence is substantially supported by the results of tagging operations.

(*a*) *Migration from the Nursery Area to Western Australia*

Since there is no commercial fishery in the Great Australian Bight, evidence of migration through this area could be obtained only from tagging operations. In all operations in the nursery areas, a white plastic internal tag was used; these tags were easily and quickly inserted, and had proved highly successful in experiments with western subspecies adults in Western Australia (Section IV(*c*)). The tags were of three sizes, and the actual size inserted was selected to suit the individual fish marked. The smallest tag was approximately 33 mm in length by 10 mm at the wider end, the intermediate size 34 mm by 14 mm, and the largest 50 mm by 25 mm. The largest tag and equipment similar to that used in these investigations have been figured by Olsen (1953). Length data and scale samples were obtained for the released fish, except in a few cases where insufficient personnel were available and it was necessary to dispense with the scale sampling and, in some cases, also the measuring of the fish. But where measuring could not be done a record was kept of the size range of the fish released.

In the period from 1952 to 1954, six tagging operations were conducted in South Australian waters. By these operations 4104 salmon were released and of these 409 were recaptured; the release and recapture data are summarized in Table 4. Of the 409 recaptures from the South Australian operations, 348 were taken in local waters and 61 in Western Australia. The Western Australian recaptures were approximately 1·5 per cent. of the total releases. The most notable result of the tagging studies was the recapture in Western Australia of eight of the 104 fish released at Kangaroo Island in 1952 (Operation 2); these recaptures represent a recovery rate of 7·7 per cent. Other operations demonstrating a large scale movement of South Australian fish to Western Australia were the release of 1912 salmon at Ceduna in June 1952 (Operation 1) and 461 salmon at Kangaroo Island in January 1954 (Operation 5) from which 41 and 8 recaptures respectively were obtained in Western Australia. The migration paths of the Western Australian recaptured fish are shown schematically in Figure 6; the shortest distance travelled was approximately 725 miles and the longest approximately 1200 miles.

In Western Australia, the salmon taken by the commercial fishery operating during the spawning phase are generally 5 to 9 years of age (Section II(*c*)). Since all these fish have mature gonads, it is evident that spawning may be accomplished by 5-year old fish. However, since the 6-year age group is the first significant group and in fact dominates the Western Australian catches, and considering also that many 5-year old fish are taken in South Australia, it is obvious that the majority

TABLE 4

SUMMARY OF TAGGING OPERATIONS CONDUCTED IN SOUTH AUSTRALIA

The ages of the released fish are those at the spawning period, February to June, in the year of release. Recaptures in South Australia are shown in ordinary type, those in Western Australia in *italics*

Operation Number	Release Data			Year Expected in Western Australia		Year of Recapture						Total Recaptures	
	Locality and Date	Number	Predominant Age Groups	As 5-Year Fish	At 6-Year Fish	1952	1953	1954	1955	1956	1957	South Australia	Western Australia
1	Ceduna	1912	2	1955	1956	11	5		1			17	
	June 1952								*28*	*8*	*4*		*40*
2	Kangaroo I.	104	2 and	1954	1955		4	2				6	
	November 1952		3	1955	1956				*5*	*3*			*8*
3	Port Noarlunga	221	1	1956	1957	28	23					51	
	December 1952												
4	Port Lincoln	172	2	1956	1957		2	1				3	
	April–May 1953												
5	Kangaroo I.	461	5	1954	1955			34	1			35	
	January 1954								*7*	*1*			*8*
6	Port Lincoln	1234	3 and	1955	1956			193	33	10		236	
	March 1954		4	1956	1957					*3*	*2*		*5*

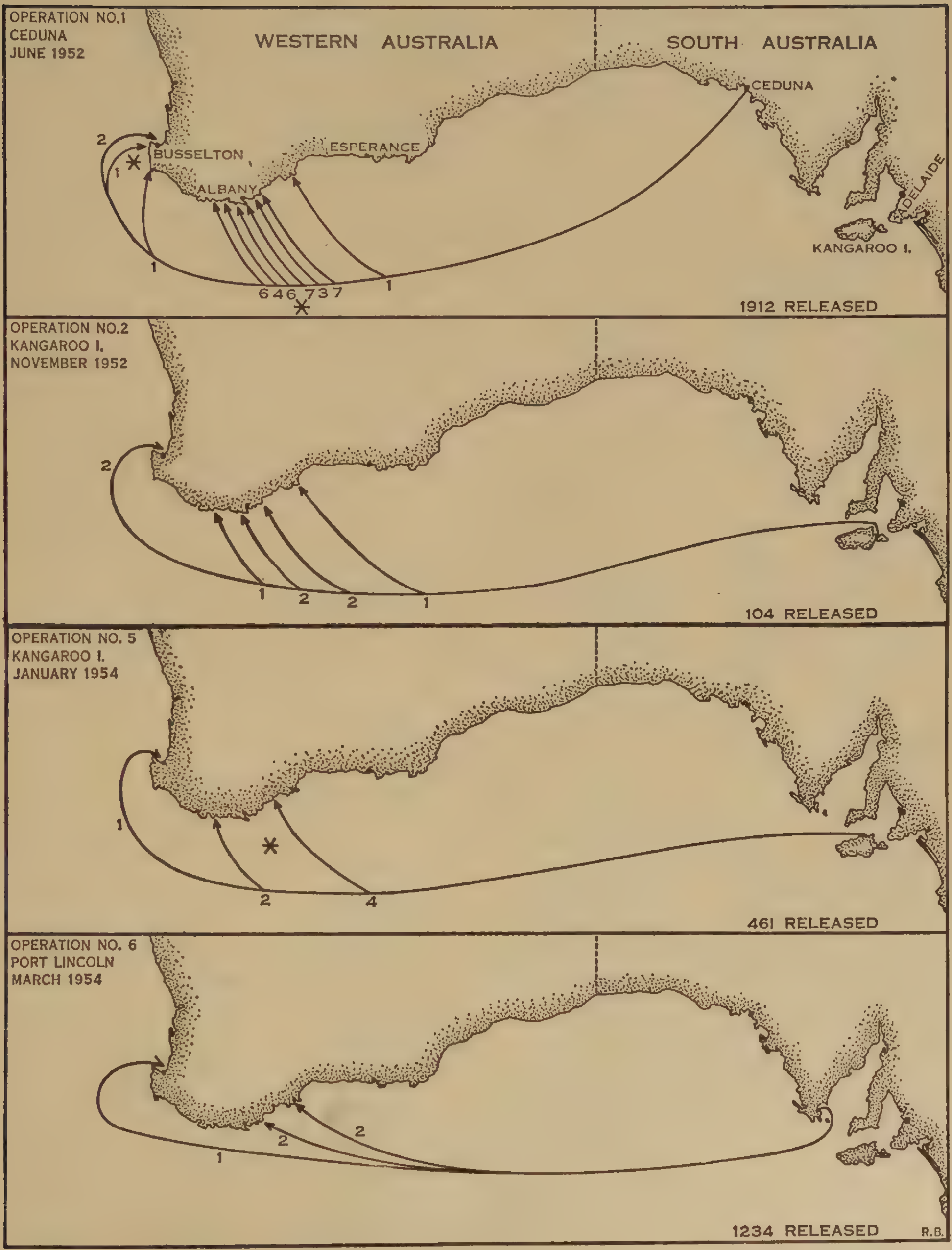
OPERATION NO.1
CEDUNA
JUNE 1952
WESTERN AUSTRALIA
SOUTH AUSTRALIA
CEDUNA
ESPERANCE
BUSSELTON
ALBANY
ADELAIDE
KANGAROO I.
2
1
*
1
6 4 6 7 3 7
*
1
1912 RELEASED
OPERATION NO.2
KANGAROO I.
NOVEMBER 1952
2
1
2
2
1
104 RELEASED
OPERATION NO. 5
KANGAROO I.
JANUARY 1954
1
*
2
4
461 RELEASED
OPERATION NO. 6
PORT LINCOLN
MARCH 1954
2
2
1
1234 RELEASED
R.B.

Fig. 6.—Migration of tagged fish from South Australia to Western Australia. The numbers denote the recaptures at each locality. * denotes a recapture without precise locality data.

of these salmon spawn first in their sixth year of life. Most of the salmon released in South Australia were from 1 to 3 years of age. Thus for most operations, it was to be expected that two or more years would elapse before recoveries would be made in Western Australia, although tagged fish would be recaptured in South Australian waters in the first years after each operation. This in fact proved to be the case; recaptures were first made in South Australia, and only after the first few years, and with a falling off in the number of these recoveries, were recaptures made in Western Australia. Conclusive evidence of migration to Western Australia

TABLE 5

SALMON RELEASED IN SOUTH AUSTRALIA AND RECAPTURED IN WESTERN AUSTRALIA

Tag Number	Release Date	Recapture Locality	Recapture Date	Days Freedom	Miles Travelled
		Operation 1: Ceduna			
2957	20.vi.52	Bremer Bay	18. i.55	942	725
2810	20.vi.52	Peaceful Bay	9. iii.55	992	865
7558	10.vi.52	Cheyne Beach	14. iii.55	1007	785
2578	19.vi.52	Cheyne Beach	17. iii.55	1001	785
2190	19.vi.52	Torbay Beach	iii –iv.55	985–1045	830
7017	10.vi.52	Torbay Beach	1. iv.55	1025	830
7395	11.vi.52	Cheyne Beach	7. iv.55	1030	785
7123	10.vi.52	Albany	*e.* iv.55*	1025–1034	815
7378	11.vi.52	Albany	*e.* iv.55	1024–1033	815
2165	19.vi.52	Albany	*e.* iv.55	1016–1025	815
7110	10.vi.52	Peaceful Bay	18. iv.55	1042	865
2593	19.vi.52	Eagle Bay	22. iv.55	1037	1020
7221	11.vi.52	Smith's Beach	v.55	1054–1084	1000
2469	19.vi.52	Boat Harbour	26. v.55	1071	855
7373	11.vi.52	Cheyne Beach	22. vi.55	1106	785
7588	12.vi.52	Cheyne Beach	22. vi.55	1105	785
63	18.vi.52	Nanarup Beach	10. vii.55	1117	810
3093	20.vi.52	Cheyne Beach	12. vii.55	1117	785
7096	10.vi.52	Parry's Inlet	15. vii.55	1130	850
7577	12.vi.52	Parry's Inlet	15. vii.55	1128	850
2890	20.vi.52	Nanarup Beach	7.viii.55	1143	810
7279	11.vi.52	Albany	21.viii.55	1166	815
2438	19.vi.52	Nanarup Beach	16. ix.55	1184	810
7124	10.vi.52	Albany	17. ix.55	1194	815
2356	19.vi.52	Denmark	18. ix.55	1186	845
2840	20.vi.52	Augusta	30. xii.55	1288	965
7148	10.vi.52	Albany Cannery†	iii –iv.55	994–1054	†
7223	11.vi.52	Busselton Area†	iii – v.55	993–1085	†
7338	11.vi.52	Torbay Beach	21. ii.56	1350	830
85	18.vi.52	Two People Bay	4. iii.56	1355	800
2431	19.vi.52	Peaceful Bay	5. iii.56	1355	865
7404	11.vi.52	Torbay Beach	13. iii.56	1371	830
2012	19.vi.52	Torbay Beach	26. iii.56	1376	830

* *e*, early. † Accurate data not available.

TABLE 5 (*Continued*)

Tag Number	Release Date	Recapture Locality	Recapture Date	Days Freedom	Miles Travelled
		Operation 1: Ceduna (*Continued*)			
2062	10.vi.52	Boat Harbour	10. iv.56	1400	855
114	18.vi.52	Parry's Inlet	11. vi.56	1454	850
7544	11.vi.52	Cheyne Beach	17. vii.56	1497	785
7101	10.vi.52	Peaceful Bay	10. iii.57	1734	865
2238	19.vi.52	Eagle Bay	20. iii.57	1735	1020
7368	11.vi.52	Torbay Beach	17. iv.57	1771	830
7425	11.vi.52	Albany	27. vii.57	1872	815
		Operation 2: Kangaroo Island (American River)			
4294	29.xi.52	Doubtful I.	17. iii.55	838	910
4233		Torbay Beach	iii.55	822–852	1000
4291		Busselton	5. v.55	887	1220
4225		Peaceful Bay	14. v.55	906	1035
4277		Cheyne Beach	22. vi.55	935	960
4216		Torbay Beach	20. ii.56	1178	1000
4268		Meelup Beach	10. iv.56	1228	1210
4243		Cheyne Beach	3. vii.56	1312	960
		Operation 5: Kangaroo Island (Emu Bay)			
4439	24. i.54	Cheyne Beach	30. iii.55	430	920
4489		Cheyne Beach	4. iv.55	435	920
4464		Parry's Inlet	iv.55	432–461	990
4500		Smith's Beach	v.55	462–492	1160
7903		Cheyne Beach	22. vi.55	514	920
7884		Cheyne Beach	1.viii.55	554	920
4480		Albany Cannery†	iv.55	432–461	†
7780		Parry's Inlet	7. iv.56	742	990
		Operation 6: Port Lincoln			
4510	25.iii.54	Bremer Bay	13. iii.56	719	840
4124	25.iii.54	Cheyne Beach	25. iii.56	731	870
3791	24.iii.54	Bremer Bay	2. iv.56	740	840
3763	24.iii.54	Cheyne Beach	iii.57	1073–1103	870
3946	25.iii.54	Meelup Beach	20. iii.57	1091	1130

† Accurate data not available.

was obtained from four of these operations. In the two other operations (3 and 4) local recaptures were made in the two years following the release of the fish, but no recoveries were made in Western Australia.

In Operation 1, scales of some of the individual fish later recaptured in Western Australia showed them to be just 2 years of age when released, so that in 1955 when these fish were recaptured they were 5 years of age. In Operation 5, most of the salmon released in January 1954 would have been 5 years of age at the 1954 spawning period (February–June), but no tagged fish were recaptured in Western Australia until 1955 when they were 6-year fish. Males of the same size group, taken from the same haul as the released fish of this operation, showed active spermatogenesis and it was thought that some of the released fish might have attempted the migration immediately after their release to participate in the 1954 spawning. However, 34 of the released fish were recaptured in South Australian waters during 1954, whereas no Western Australian recapture was made until 1955, which suggests that the fish did not migrate to the spawning area until just before the 1955 spawning season. Although it was thought that active spermatogenesis would have meant that these fish were about to commence the migration to the spawning area in Western Australia, it obviously did not; the presence of degenerative changes in the testes of the larger fish in South Australia in April, as discussed in an earlier section, shows that spermatogenesis may take place in non-migratory males (Section III(*b*)).

Since 1951 commercial fishing has been done chiefly in the area from Bremer Bay to Busselton, and even in this area intensive fishing operations were carried out from 1955 to 1957 only between February and July when the salmon schools were engaged on pre-spawning and post-spawning migrations (Section IV(*c*)). Consequently tagged fish from South Australia were recovered only between Bremer Bay and Busselton (Table 5 and Fig. 6) and within the limited period of the fishery. Because no short term recaptures were obtained in Western Australia, and the fishery in that area operated over such a short period each year, it was impossible to determine the precise arrival time in Western Australia of maturing fish from South Australia. Nevertheless the evidence suggests that the movement of juveniles from the nursery area is so timed that these fish move along the southern coast of Western Australia between February and April, and that the schools engaged on pre-spawning migration, on which the commercial fishery in Western Australia operates, are made up of fish that have just arrived from the nursery area, and of fish that have spawned previously and have been distributed along the southern coast of Western Australia during the non-spawning phase (Section IV(*c*)).

(*b*) *Migration within the Nursery Area*

(i) *South Australian Operations.*—Two tagging operations conducted in South Australia, at Port Noarlunga in December 1952 and Port Lincoln in March 1954, yielded a high percentage of local recoveries (Table 4). From the Port Noarlunga releases, 51 were recaptured to yield a recovery rate of 23·1 per cent. and, with the exception of a single fish that moved northwards to the Adelaide region (Table 6), all the recaptures were taken within a few miles of the release locality. Two recaptures were made on the beaches near Port Noarlunga, while 45 of the tagged fish were caught at the release beach. The remaining two tags were recovered at the Adelaide market; no accurate locality data are available for these, but the market receipts indicate that the fish were recaptured in the Port Noarlunga area. Of the 45 fish taken at the point of release, 25 were recaptured within 25 days, a further 18 were taken by the end of 52 days, and the remaining two tags were recovered after 169 days of freedom. Since a similar recovery pattern normally

TABLE 6

MOVEMENTS OF TAGGED SALMON RELEASED AND RECAPTURED IN SOUTH AUSTRALIA

Operation Number	Release Locality	Release Date	Recapture Locality	Recapture Date	Number Recaptured	Days Freedom	Miles Travelled
1	Ceduna	20.vi.52	Streaky Bay	7. x.52	1	109	70
2	Kangaroo I.	29.xi.52	Port Noarlunga	9. i.54	1	406	50
3	Port Noarlunga	5.xii.52	Adelaide Harbour	30. xii.52	1	25	25
4	Port Lincoln	1. v.53	Cowell	15. ix.54	1	501	80
5	Kangaroo I.	24. i.54	Middle R. Area	8. iv.54	1	74	25
			Middle R. Area	12. iii.54	1	47	25
			Penneshaw	19.viii.54	1	207	25
			Rapid Bay	23. iii.54	1	58	35
			Wedge I.	16. iii.55	1	416	60
			Cowell	15. ix.54	1	234	135
6	Port Lincoln	24. iii.54	Tumby Bay	20. iv.54	17	27	25
		25. iii.54	Tumby Bay	20. iv.54	2	26	25
		25. iii.54	Port Pirie	23. vi.54	1	90	140
		24. iii.54	Whyalla	18. vii.54	1	116	140
		25. iii.54	Port Pirie	10.viii.54	1	138	140
		25. iii.54	Cowell	15. ix.54	3	174	80
		25. iii.54	Wallaroo	23. ix.54	1	182	100
		25. iii.54	Cowell	29. ix.54	2	188	80
		24. iii.54	Cowell	17. x.54	1	207	80
		24. iii.54	Port Neill	30. x.54	1	220	45
		25. iii.54	Port Neill	30. x.54	3	219	45
		24. iii.54	Wedge I.	16. ii.55	1	329	40
		24. iii.54	Cowell	28. x.55	2	583	80
		24. iii.54	Cowell	11. i.56	9	658	80
		25. iii.54	Cowell	11. i.56	1	657	80

was obtained when tagging operations were conducted at Hopetoun in Western Australia during the non-spawning phase (Section IV(*c*)), perhaps the school behaviour pattern there, which was observed regularly from the shore, affords an explanation of the recovery trend at Port Noarlunga. At Hopetoun, a large school was generally visible in an inaccessible position a little distance from the release area, and the tagged fish joined this school. Subsequently, small portions of this school broke off and moving inshore were netted, and a large number of short-term local recaptures was obtained. A high recovery rate of the released fish persisted until the main school moved to sea, after which only occasional recaptures were made at the point of release.

In the Port Lincoln operation, 1234 fish were released and 236 (19·1 per cent.) were recaptured in South Australian waters. Of these recoveries, 46 showed movement throughout the Spencer Gulf region, while 190 were taken in the Port Lincoln area. Although South Australian catch statistics are incomplete and inaccurate, sufficient is known to show that probably about 40–60 per cent. of the catch has been taken in the Port Lincoln area and the total catch has been of the order of 500 tons per annum. It is evident from the number of schools observed inshore that salmon are abundant in the approach areas of Spencer Gulf; feeding evidently takes place at sea but, from time to time, schools appear inshore and lie-up for periods lasting from days to weeks at preferred reefs and beaches in the Port Lincoln area. These preferred points are well known to the fishermen who move from point to point and conduct an intense fishery on the inshore schools. Many of the local recaptures recorded in the Port Lincoln operation were taken soon after release; 74 fish were recaptured within 50 days of release, a further 61 fish were taken between 50 and 100 days, while the remaining 55 fish were free for periods ranging from 129 to 576 days. For several months after the release of the salmon, groups of tagged fish were recaptured in the schools netted in the Port Lincoln area. It is apparent that when the tagged fish were released, they dispersed throughout the area and joined other schools. A high recovery rate was recorded when these schools, moving inshore to lie-up at the preferred points, were netted.

The hypothetical migration paths of fish released and recaptured in South Australia are shown in Figure 7; these paths show a general dispersion, particularly throughout the Gulf areas. Although it is impossible to demonstrate, from the tagging results, any precise seasonal movement of South Australian fish, recoveries from Operation 6 (Table 6) indicate a northerly movement of salmon in Spencer Gulf in the period from April to October. Recaptures were recorded from Tumby Bay in April, from Port Pirie and Whyalla between June and August, and from Wallaroo and Cowell in September and October. The recaptures at Cowell in September 1954 of fish released at Kangaroo Island in January 1954 (Operation 5) and Port Lincoln in April 1953 (Operation 4) support the suggestion of a northerly movement into Spencer Gulf, while recaptures in December 1955 and January 1956 (Operation 6) indicate that the period of the northerly penetration may extend into December and January, or may vary from year to year. However, it is not known whether the recaptures in the more northerly areas of Spencer Gulf reflect the activity of the fishery or the movements of the fish.

(ii) *Tasmanian and Victorian Operations.*—An exact analysis cannot be made of the results of the Tasmanian and Victorian tagging studies because both subspecies occur in the schools in these areas and it was not possible to distinguish the two forms in the tagging operations.

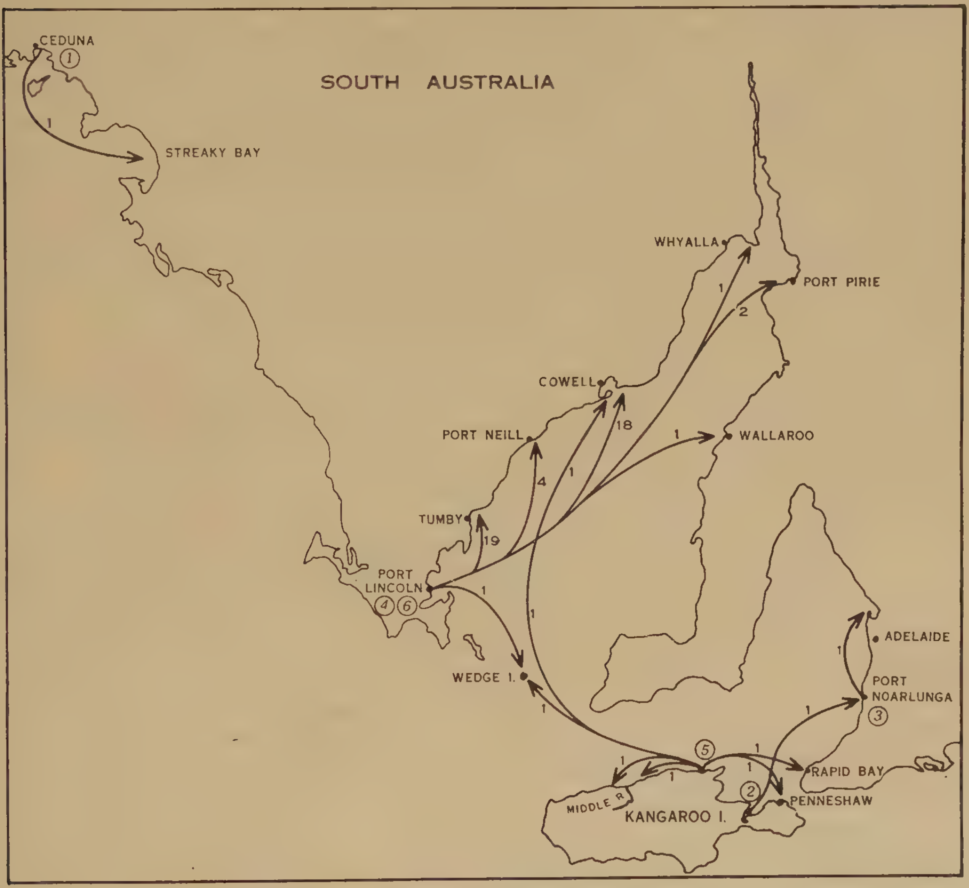
CEDUNA
①
SOUTH AUSTRALIA
1
STREAKY BAY
WHYALLA
1
PORT PIRIE
2
COWELL
18
PORT NEILL
1
WALLAROO
4
1
TUMBY
19
PORT LINCOLN
④ ⑥
1
1
ADELAIDE
1
WEDGE I.
PORT NOARLUNGA
③
1
1
⑤
1
1
1
RAPID BAY
1
②
PENNESHAW
MIDDLE R.
KANGAROO I.

Fig. 7.—Dispersion of tagged salmon in South Australian waters. The tagging operation numbers are circled. The other numbers denote the recaptures at each locality.

In the period from 1949 to 1952, 935 salmon were released in Tasmania in seven operations (Table 7) and with perhaps the exception of the Arthur River releases, it is probable that both eastern and western subspecies were liberated in all operations. In conjunction with most tagging operations, gill rakers were examined from a sample of salmon from the same haul as the released fish, and from these data and the data on the general distribution of the subspecies in Tasmanian waters (Table 1), an estimate was made of the number of each subspecies released in each operation. It is estimated that approximately 500 to 600 fish of the western subspecies were released in the Tasmanian operations, and age determinations made on fish from the same hauls indicated that the western subspecies salmon released

TABLE 7

SUMMARY OF TASMANIAN TAGGING OPERATIONS, RELEASES, AND RECAPTURES

Operation Number	Release Locality and Period	Release No.	Local Recoveries	Migrant Fish					
				Release Date	Recapture Locality	Recapture Date	Days Freedom	Miles Travelled	Designated Subspecies
1	Partridge I. January 1949	83	4						
2	Dunalley January 1949	91	3	28. i.49	Triabunna	10. ii.49	13	25	Eastern or Western
					Hobart	12. iv.49	74	30	
3	Dunalley October 1952	132							
4	St. Helens October 1952	228	2	24. x.52	Eden	12. v.53	200	260	Eastern
					Eden	vi.53	220–249	260	Eastern
					Merimbula	27. vii.53	276	290	Eastern
					Lakes Entrance	vii.53	250–280	210	Eastern
					Merimbula	22. iii.54	514	290	Eastern
					Babel I.	iv.54	522–551	80	Eastern
					Babel I.	iv.54	522–551	80	Eastern
					Merimbula	5. vii.54	619	290	Eastern
					Mallacoota	27.viii.54	672	230	Eastern
					Mallacoota	27.viii.54	672	230	Eastern
					Eden			260	Eastern
5	Port Sorell October 1952	286	7	19. x.52	Eden	vi.53	225–254	300	Eastern
					Hunter I.	iii.54	498–528	90	Western
6	Arthur R. January 1953	88		9. i.53	Macquarie Harbour	10. v.53	121	80	Western
7	Arthur R. March 1955	27		23.iii.55	Lorne	31. v.57	800	150	Western
					Lakes Entrance	vii.57	831–861	265	Western

were predominantly 2 and 3 years of age. No recaptures of Tasmanian released fish were recorded from Western Australia, but a considerable number moved from the locality at which they were tagged. Because it was not possible to distinguish the subspecies during the tagging operations, and recaptured fish were not returned with the tag, migrations cannot be designated conclusively to one or other of the subspecies.

The Tasmanian operation demonstrating migration most conclusively was the release of 228 salmon at St. Helens in October 1952 (Table 7). Eleven migrant fish were recaptured, two at Babel Island, three in eastern Victoria, and six in New South Wales (Fig. 8). These areas are occupied either exclusively or predominantly by eastern subspecies adults (Fairbridge 1950), and the results are therefore held to furnish information on the migrations of the eastern form. This is in agreement with the gill raker data collected at the time of release which indicated that the eastern subspecies was the predominant form. The release of 286 fish at Port Sorell yielded only two migrants; one fish was recaptured in New South Wales, the other in the Hunter Island area. The New South Wales recapture is considered to have been an eastern subspecies because this area is occupied exclusively by the eastern group, and it is estimated that approximately 20 per cent. of the Port Sorell releases comprised the eastern form. The Hunter Island return, captured in March 1954,

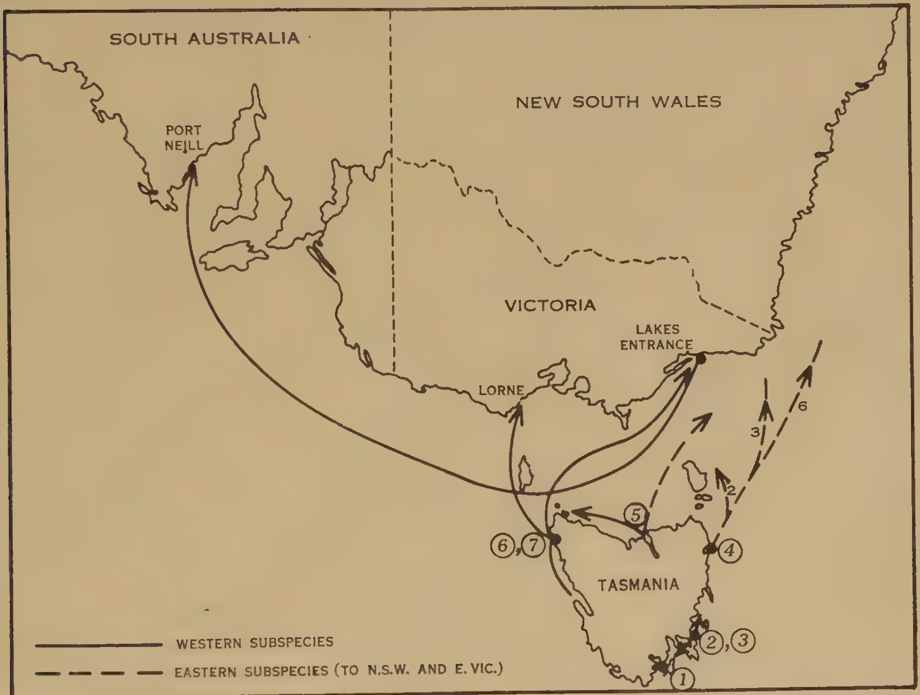

Fig. 8.—Migration, attributed to western subspecies of salmon, from Tasmanian and Victorian waters. The tagging operation numbers are circled. The other numbers denote the recaptures at each locality.

would seem to have been a western subspecies because this form comprised the major part of the releases and predominates in the more westerly regions of Tasmania. No recaptures showing movement were obtained for the Partridge Island releases, and only two migrants were recorded for the operations conducted at Dunalley. These fish, released in January 1949, were recaptured at Triabunna and Hobart soon after release; it is not possible to attribute the movements to one or other subspecies because both subspecies were released in the Dunalley operations and occur with reasonable frequency in both recapture areas.

Three salmon showing movement were recaptured from among 115 salmon released at Arthur River (Table 7) and because the releases are believed to have been almost exclusively western subspecies, the recoveries are held to furnish evidence on the migrations of this form. One fish, released in January 1953, was recaptured in May 1953 at Macquarie Harbour (Fig. 8), while two fish, released in March 1955, were recaptured in Victorian waters; one recapture was recorded at Lorne in May 1957, the other at Lakes Entrance in July 1957. The western subspecies is the predominant form in the Lorne area, while reasonable numbers of the western subspecies are found at all times of the year in the Lakes Entrance area.

The fishing operations in the western areas of Victoria are so sporadic that it was impossible to arrange for the release of western subspecies juveniles in that area. However, a tagging operation at Lakes Entrance intended to analyse the seasonal movement of the eastern subspecies adults yielded a recapture that must be held to represent the movement of fish of the western subspecies of that area. Schools taken in the Lakes Entrance area in the autumn normally comprise the eastern form, but invariably contain a small percentage of western subspecies juveniles. Of 300 fish released in April 1952, 27 recaptures were recorded in New South Wales between June and October; this confirmed the belief in a northerly movement of the eastern subspecies adults. However, in October 1954 one fish was recaptured at Port Neill in South Australia (Fig. 8). Because South Australia is out of the normal range of the eastern subspecies, the fish that carried the tag is thought to have been of the western form. It might have been an aberrant eastern subspecies individual but even so its movement illustrates the path along which the numbers of western subspecies individuals known to spend some time in the Lakes Entrance area could travel to regain the normal distribution area of the western form.

(c) *Migration within the Adult Area*

The present understanding of the behaviour of the western subspecies adults is that they spawn within the period from February to June, and whilst it seems possible that some fish may spawn between Hopetoun and the Parry's Inlet area, evidence has been put forward to suggest that the principal spawning area is centred between Cape Leeuwin and Busselton (Section III). Between July and January, the non-spawning phase, the adult fish are lying chiefly in the area between Bremer Bay and Esperance, and in order to reach the principal spawning area, these fish must migrate westward. This westerly movement commences in February and apparently has been accomplished by mid April by all fish that will spawn in a particular year. After spawning the fish return to the non-spawning area, i.e. they move in an easterly direction in a migration that seems to begin in mid May and be over, in most years, by July. The movement of the schools in these migrations is observed from the beaches, and that the migrations are involved in the reproductive habits of the fish and are characteristic of the entire population is indicated by evidence from the commercial fishery catches and tagging as discussed below.

(i) *Evidence from the Commercial Fishery.*—In Western Australia the commercial fishery is organized to operate over the whole coastline from the Perth area to about 130 miles east of Esperance. The fishermen combine in teams, usually 6 to 12 men, and normally operate in definite areas; an area may comprise a single beach or a stretch of coastline. Small boats and beach seines, which are moved from point to point on the coast by road are operated from the beaches.

In the non-spawning phase the teams operate in a manner different from that in the spawning phase. In the former, when the only apparent movement is inshore–offshore and the schools lie-up on the beaches for periods of a few days to several weeks, the fishing teams keep a watch on the beaches in their area and net the schools as they are observed. During the spawning phase when the fish are actively migrating along the coast, each team normally occupies a beach and awaits the appearance of travelling schools.

Throughout the year, there is constant observation for fish, and the net is shot only when fish are observed. Therefore, the spotting observation is the principal determinant of catch. However, there are occasions when schools are observed but cannot be netted. It may not be possible to reach the beach by road or the school may be lying out of range of the beach seine; even when the school is close inshore, heavy surf or an unsatisfactory hauling area may prevent the shooting of the net. No records are kept by the fishermen of the occasions on which they have been unable to make a shot at or to capture a school observed. Moreover, no observing or fishing is done at night, so there is no measure of the night visits of schools. In spite of the above reservations these records of occurrences and the catch of the fishery yield reliable evidence on the behaviour of the schools. Their value as a means of comparing abundance between years will be discussed in another paper. A summary of the data on school occurrences and fishing activity in the main fishing areas, together with seasonal gonad activity and school movements, is shown in Table 8.

Aerial and beach observations indicate that in the spawning phase (February to June) most inshore schools are distributed in the Bremer Bay, Cheyne Beach, Parry's Inlet, and Busselton areas (Fig. 9). The seasonal abundance of salmon in these areas has long been known to the fishermen, but prior to the establishment of local canneries in 1947, little fishing was done. Active fishing commenced then, and an intensive beach seine fishery has since operated in all areas. Almost the whole annual catch in the main areas between Bremer Bay and Busselton has been taken in the spawning phase period (Figs. 10 and 11).

In the non-spawning phase the schools appear in the more easterly regions of the distribution, but very few show in the Busselton and Parry's Inlet areas. However, whereas the spawning phase distribution has remained constant at least since 1947, changes appear to have occurred in the non-spawning phase distribution.

Table 8

SUMMARY OF THE DATA ON SCHOOL OCCURRENCES AND FISHING ACTIVITY IN THE MAIN FISHING AREAS, TOGETHER WITH SEASONAL GONAD ACTIVITY AND SCHOOL MOVEMENTS

Month	Gonad Condition	Direction of Movement	School Occurrences and Fishing Activity				
			Hopetoun Area	Bremer Bay Area	Cheyne Beach Area	Parry's Inlet Area	Busselton Area
February	Period of active pre-spawning development	Schools moving westward along southern coast, then northward towards Busselton area	No school occurrences or fishery	Schools numerous and large, moving in a westerly direction Active fishery with peak in March			No school occurrences or fishery
March							Schools numerous with active fishery. Peak in April
April							
May	Pre-spawning and post-spawning activity	Converse movement by most schools. Some schools may move northwards to the Perth area	Season for school occurrences and fishery Fishery peak in July and August	Schools in reasonable numbers, but small, moving in an easterly direction Active fishery with peak in June			
June	Post-spawning degeneration						
July	Period of gonad quiescence						Occasional schools
August		Inshore-offshore movement by most schools. Probably southerly and easterly movement by schools from Perth area		Reasonable number of schools in recent years. Sporadic fishing operations		Occasional schools	
September October November December January							

Between 1945 and 1951, the main concentration of inshore schools occurred in the Bremer Bay, Hopetoun, and Esperance areas, while in more recent years the only occurrence of any number of schools on the beaches has been in the Cheyne Beach and Bremer Bay areas.

Commercial fishing operations in Western Australia commenced at Hopetoun in 1945. This fishery, which operated in the non-spawning phase (Fig. 10), reached its peak in 1948, then declined, and finally ceased in 1952 (Fig. 11). The Hopetoun fishery was confined to a single beach, and was concentrated on schools moving inshore and lying-up on the beach; the beach was sheltered by reef, and provided excellent seining conditions. Throughout the non-spawning phase, a large school of salmon was invariably found lying-up in an inaccessible position outside the reef but, day by day, small portions of the main school broke off and were netted when they moved inside the reef. While the Hopetoun fishery was operative, many schools were reported in the Bremer Bay, Hopetoun, and Esperance areas, which were regarded as the non-spawning phase distribution of the adult stock in those years. In 1948 and 1949, roads were constructed to many of the beaches east of Esperance, and some fishing took place. The decline of the Hopetoun fishery is often attributed to the intense fishery on a single beach, the schools being said to vacate the beach because of net-shyness, pollution of the beach by the cleaning operations, or other local factors. However, the failure of the Hopetoun fishery was coincident with the disappearance of the non-spawning phase schools on the beaches throughout the Hopetoun and Esperance areas. Although the failure of the Hopetoun fishery could well have been caused by some local factor, it is inconceivable that local factors were responsible for the disappearance of the schools from the whole of the Hopetoun and Esperance areas. It is probable that there has been a change in the non-spawning phase distribution because since 1951, the main

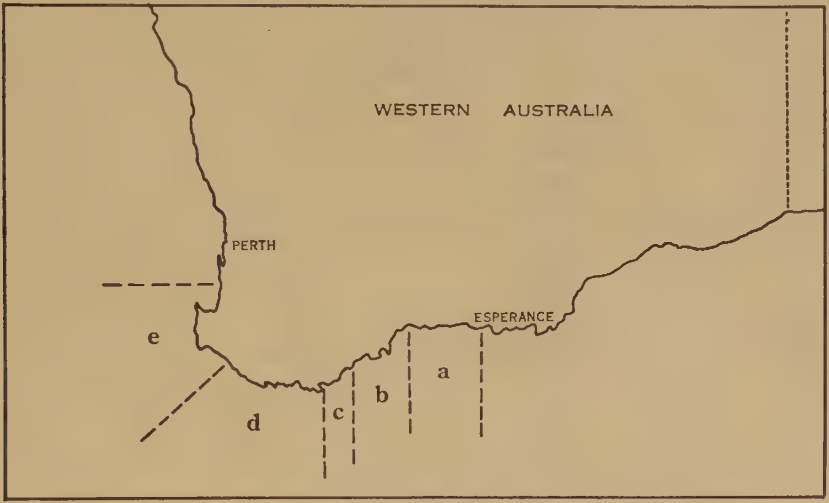

Fig. 9.—Main areas of commercial fishing in Western Australia: *a*, Hopetoun; *b*, Bremer Bay; *c*, Cheyne Beach; *d*, Parry's Inlet; *e*, Busselton.

concentration of inshore schools has been in the Cheyne Beach and Bremer Bay areas. Many of the preferred lying-up points in these areas are inaccessible, and the non-spawning phase catch has been almost negligible since the failure of the Hopetoun fishery. However, it is possible that most schools still occur in the Bremer Bay, Hopetoun, and Esperance areas during the non-spawning phase, but they remain offshore and their absence from the beaches has led to false conclusions regarding distribution.

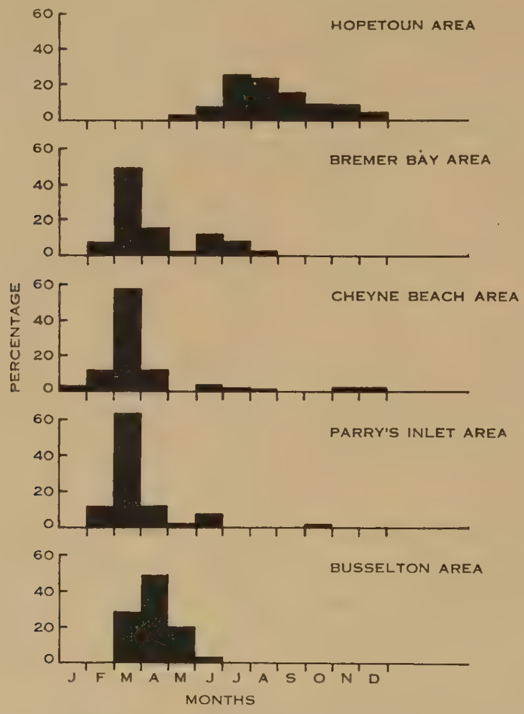

Fig. 10.—The 1945–54 commercial catch of Australian salmon in the main fishing areas of Western Australia. For each month the area catch is expressed as a percentage of the total catch in the area for the 1945–54 period; monthly catches representing less than 2 per cent. of the total area catch are not shown.

The fishery commences on the beaches in the Bremer Bay, Cheyne Beach, and Parry's Inlet areas in late February, reaches its peak in March, and declines in April (Fig. 10). This fishery is operative on schools moving in a westerly direction. The small catches in the Cheyne Beach area in January were from stationary schools, since this area has been part of the non-spawning phase habitat in recent years. Catches taken in May in any of these areas are normally taken at the end of the month, and comprise fish already undertaking the easterly post-spawning migration. In the Busselton area there is no active fishery in February. The fishery commences in March, reaches a peak in April, declines in May, and finally ceases in June (Fig. 10). The fishery in the Parry's Inlet, Cheyne Beach, and Bremer Bay areas recommences at the end of May, but now operates on schools participating in the post-spawning migration. This fishery reaches its greatest intensity in June, and may operate throughout July, but the quantity of fish taken is small compared with the catches during the pre-spawning migration.

An abundance of salmon is reported occasionally in the Perth area immediately after the spawning season. It is evident that although the main post-spawning migration is eastwards, in some years part of the population moves northwards immediately after spawning. Observations on school occurrences suggest that these fish subsequently move southwards and eastwards to the non-spawning distribution area.

(ii) *Evidence from Tagging.*—In Western Australia tagging operations were conducted in most instances on the surf beaches; the salmon were obtained from the beach hauls of the commercial fishermen. The fish were captured individually from within the net and immediately tagged and released because the action of the surf and the large size of the fish generally precluded the use of holding cages. A tag was required that could be easily and quickly attached because only a limited period of time existed to complete the operation. A monel metal operculum strap tag was used in the early operations. This tag could be attached satisfactorily under the adverse tagging conditions, but because few long-term recoveries were made, it was concluded that the tag worked free of the operculum. Petersen disk tags proved unsuitable, and since 1951 white plastic internal tags (Section IV(*a*)) have been used for all operations. These tags proved ideal except that length data for the recaptured fish are obtained only rarely because normally the fish are beheaded before gutting.

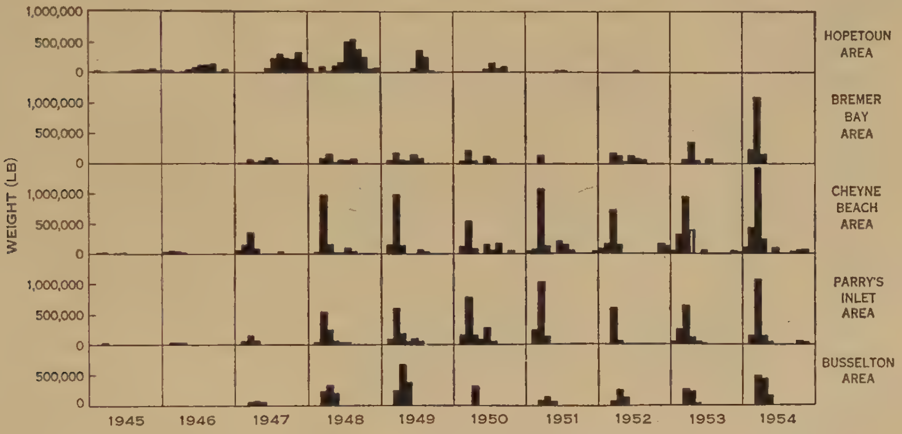

Fig. 11.—Monthly catch in each year (1945–54) for main fishing areas in Western Australia.

In the period from 1945 to 1949, tagging operations were conducted at Hopetoun, and to a limited extent Esperance, during the non-spawning phase. Only local recaptures were obtained and hence these operations did not furnish evidence of the westerly pre-spawning migration, probably because the number of fish released each year was small in relation to the spawning phase catch in those years (Fig. 11). At Hopetoun a large number of short-term recaptures was made. In many instances small portions of a large school lying-up out of range of the beach seines broke off, and moving inshore, were netted. Many of the salmon tagged and released from such hauls returned to the main school, and were subsequently taken as short-term local recaptures as further small portions of the main school moved inshore and were netted. The overall recovery rate of all tagging operations conducted at Hopetoun during the non-spawning phase was 24 per cent.; of these recoveries, 60 per cent. were made within 14 days of release, and a further 18·5 per cent. were retaken by the end of 28 days. Once the main school moved to sea, only occasional recaptures were recorded. These were taken at the point of release when further schools moved inshore to this point, but the sporadic recovery of the tagged fish is taken to mean that when the original school moved to sea some dispersion took place and the tagged fish were distributed over a number of schools.

In the period from 1950 to 1955, tagging operations were conducted annually at the onset of the westerly pre-spawning migration; where possible, the tagging was carried out in late February or early March. The majority of the operations were conducted at Cheyne Beach and Parry's Inlet where the catches were large and regular. Access to the beaches in the Bremer Bay area at the easterly limit of the spawning phase distribution was difficult, and the catches on any one beach in the area were somewhat sporadic. In 1950, some fish were released at Cape Riche Beach but because the catches were small in later years the area was not satisfactory for the regular release of fish. The number of fish released in any one operation was limited by the cost of the large fish. In 1950 and 1951, approximately 400 fish were released each year, but when confirmation of the suggested pre-spawning migration was obtained from these operations, the number released annually was reduced to 100.

Between 1950 and 1955, 1099 salmon were released in the period from February to April, and 284 recaptures were made to give a recovery rate of 25·8 per cent. Of the 284 recaptures, 21·5 per cent. showed movement whereas the remaining 78·5 per cent. were taken at the point of release. The high recovery of tagged fish at the point of release can be explained by observation on the behaviour of many of the large schools at the onset of the pre-spawning migration. These schools move inshore and lie-up on the coast for a period lasting from a few days to perhaps several weeks before commencing the westerly migration. The large school tends to change its identity; small schools moving along the coast join the main school while, from time to time, small portions of the main school break off and move in a westerly direction. The local recaptures from operations conducted at the onset of the pre-spawning migration were obtained soon after release, and a high recovery rate normally was recorded when a large school remained stationary, in a position inaccessible to the fishermen, at the eastern end of a beach. It is evident that many if not most of the tagged fish released at the beach moved back to join this school. Subsequently, as small portions of the main school moved along the beach and were netted, the recently released fish were captured. Of the local recaptures of tagged fish released during the pre-spawning phase, 74·4 per cent. were taken within 14 days of release and 92·4 per cent. within 28 days. The remaining 7·6 per cent. were taken during the period of the post-spawning migration or in later years. In one experiment conducted at Cheyne Beach, of 119 fish released, 85 were recaptured to yield a recovery rate of 71·4 per cent. With the exception of five fish that showed movement, the recoveries were made at the point of release; 75 of these were taken within 15 days, four were taken on the twenty-second day, while the remaining fish was recaptured after two years of freedom.

Short-term recoveries only are useful as evidence of the westerly pre-spawning migration because the data provided by observation of the schools and the catch returns of the fishery show that an easterly post-spawning migration is accomplished between May and July. Thus, although 61 recoveries showing movement were obtained from the operations conducted at the onset of the pre-spawning migration, only 43 of these were made soon after release. The remaining recaptures were made west of the release localities in subsequent seasons, or east of the release localities some considerable time after the operations were conducted. The latter fish had presumably participated in the pre-spawning migration to the spawning area, and then the post-spawning to the non-spawning phase distribution, before they were recaptured.

Of the operations conducted at the onset of the pre-spawning migration, only two failed to yield short-term recoveries indicating movement. These operations comprised the release of 11 fish at Cheyne Beach on March 9, 1952, and 52 at Parry's Inlet on April 10, 1954. The remaining operations and the short-term recoveries showing movement are listed in Table 9; the migration paths of the recaptured fish are depicted in Figure 12.

The tagging results provide evidence of the suggested pre-spawning migration because, with the exception of a single fish, all the short-term local recaptures showing movement were taken west of the release locality. Consistent results were obtained for all years in which a reasonable number of fish were released. Since the number released was by no means large, the number of recoveries which showed movement is held to be indicative of a large-scale migration along the coast. The fact must be taken into account that of the 1099 salmon released, 206 of the potential migrants were removed from the population as short-term local recaptures before they had attempted or continued the pre-spawning movement.

A fish migrating from Cheyne Beach to Hamelin Bay in 14 days attained the maximum average rate of movement of approximately 15 miles a day. The overall average rate of movement, as indicated by the tagging studies, was of the order of 4 or 5 miles a day. With the exception of the fish that moved from Cheyne Beach to Hamelin Bay in 14 days, the time taken for fish to reach the Busselton area from either Cheyne Beach or Parry's Inlet ranged from 3 to 5 weeks. A similar rate of movement is indicated by the fishing intensity, because the fishery in the Busselton area reaches its peak approximately a month later than the fishery operating in the Bremer Bay, Cheyne Beach, or Parry's Inlet areas (Fig. 10).

The only short-term recapture showing an easterly movement was a fish released at Cheyne Beach on March 4, 1951, and recaptured at Cape Riche 7 days later (Table 9). The March 4 operation, which was discussed earlier, comprised the release of 119 fish of which 79 were retaken as local recaptures within the next few weeks. It is apparent that the majority of the fish released in this operation

TABLE 9

SUMMARY OF TAGGING OPERATIONS AND RECOVERIES FROM WHICH EVIDENCE OF THE PRE-SPAWNING MIGRATION IS OBTAINED

Release Data				Recovery Data			Direction	Miles	Days Freedom
Year	Locality	No.	Month	Locality	No.	Month			
1950	Cape Riche	65	Mar.	Cheyne Beach	7	Mar.	W.	30	3–17
				Peaceful Bay	2	Apr.	W.	105	31
	Parry's Inlet	338	Mar.	Boat Harbour	3	Mar.–Apr.	W.	5	0–14
				Peaceful Bay	6	Mar.–Apr.	W.	10	10–16
				Hamelin Bay	1	Apr.	W.	140	32
1951	Cheyne Beach	244	Feb.–Mar.	Cape Riche	1	Mar.	E.	30	7
				Torbay	4	Mar.	W.	50	10–14
				Peaceful Bay	3	Mar.–Apr.	W.	80	14–60*
				Hamelin Bay	1	Apr.	W.	210	33–62*
	Parry's Inlet	136	Mar.	Peaceful Bay	3	Mar.	W.	10	1–16
				Nornalup	1	Mar.	W.	25	22
				Hamelin Bay	2	Mar.–Apr.	W.	140	21, 25
1953	Cheyne Beach	99	Feb.	Boat Harbour	1	Mar.	W.	75	18
				Hamelin Bay	2	Mar.–Apr.	W.	210	14, 30
1954	Cheyne Beach	54	Mar.	Parry's Inlet	3	Mar.–Apr.	W.	70	7–17
				Hamelin Bay	1	Apr.	W.	210	38
1955	Cheyne Beach	100	Mar.	Torbay	2	Mar.	W.	50	0–16*

* Approximate date of recapture available only.

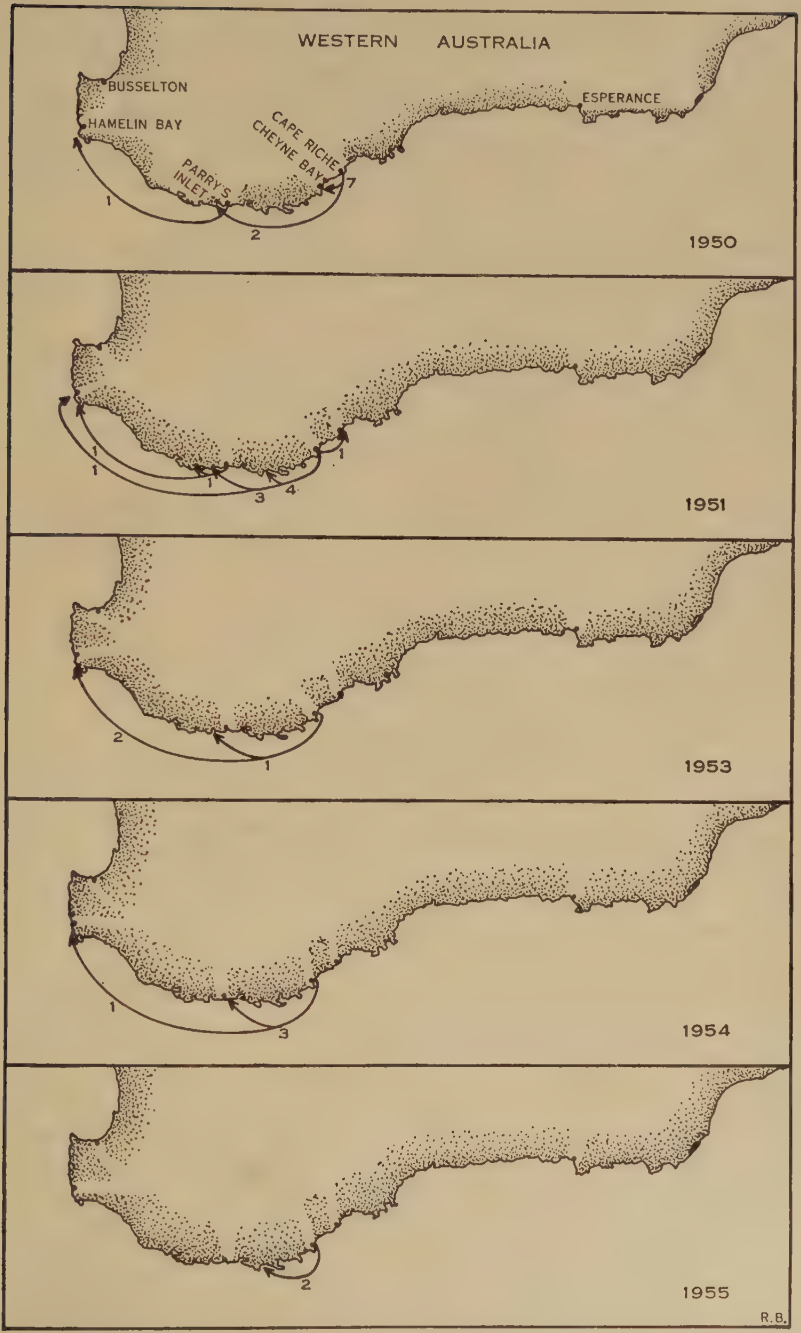
WESTERN AUSTRALIA
BUSSELTON
HAMELIN BAY
PARRY'S INLET
CAPE RICHE
CHEYNE BAY
ESPERANCE
7
1
2
1950
1
1
1
1
3
4
1951
2
1
1953
1
3
1954
2
1955
R.B.

Fig. 12.—Pre-spawning movements of Australian salmon tagged in Western Australia. Only movements of 25 miles or more are shown. The numbers denote the recaptures at each locality.

TABLE 10

SUMMARY OF TAGGING OPERATIONS AND RECOVERIES FROM WHICH EVIDENCE OF THE POST-SPAWNING MIGRATION IS OBTAINED

Release Data				Recovery Data				Direction	Miles	Days Freedom
Year	Locality	No.	Month	Locality	No.	Month	Year			
1949	Cheyne Beach*	52	Mar.	Hopetoun	1	July	1949	E.	110	116
				Esperance	1	Nov.	1949	E.	200	247
	Hamelin Bay	95	May	Hopetoun	1	July	1949	E.	315	73
				Chatham I.	1	July	1949	E.	95	72
	Parry's Inlet	26	June	Dillon Bay	1	Mar.	1950	E.	125	258
	Boat Harbour	74	June	Cheyne Beach	1	Feb.	1950	E.	75	224
1950	Parry's Inlet*	338	Mar.	Hopetoun	1	Aug.	1950	E.	180	156
				Cheyne Beach	3	May–Sept.	1950	E.	50	61–173
1954	Cheyne Beach*	54	Mar.	Bremer Bay	1	Jan.	1955	E.	65	307
	Parry's Inlet*	52	Apr.	Cheyne Beach	1	June	1954	E.	70	67
				Bremer Bay	1	Jan.	1955	E.	135	283
	Eagle Bay	51	May	Cheyne Beach	2	Oct.–Nov.	1954	E.	255	160–193
1955	Eagle Bay	102	May	Chatham I.	1	Sept.	1955	E.	145	137
				Cheyne Beach	1	June	1955	E.	255	42
				Safety Bay	1	June	1955	N.	90	36
				Bunbury	1	Aug.	1955	N.	30	84

* Operations conducted during period of pre-spawning migration.

had not continued their westerly movement, but had moved back along the coast to join oncoming schools. This would account for the large number of local recaptures at Cheyne Beach and the recovery at Cape Riche. The general results of the tagging experiments, and observations on the movement of the schools along the beaches, do not support any suggestion of a large-scale easterly movement in the period from February to April.

Tagging operations in relation to the post-spawning migration were initiated in 1949 when 224 salmon were released in the Busselton and Parry's Inlet areas in May and June. Since then only a few operations have been conducted, and all in the Busselton area. Since the failure of the Hopetoun and Esperance fisheries in the 1950–51 period, only occasional catches of salmon have been made in the non-spawning phase; the absence of a fishery during the non-spawning phase has jeopardized the chances of success from tagging operations designed to provide evidence of the suggested post-spawning migration. The operations and the recaptures from which evidence of the post-spawning migration was obtained are shown in Table 10; the migration paths of the recaptured fish are shown in Figure 13.

The results of the operations conducted in 1949 provided evidence that the post-spawning migration in that year comprised a movement from the Busselton area to the more easterly limits of the known area of adult distribution. A fish released at Hamelin Bay was recaptured at Esperance and had travelled 315 miles in its 73 days of freedom. Easterly movements are also shown by two fish from a Cheyne Beach tagging operation conducted at the onset of the pre-spawning migration, and fish released at Parry's Inlet and Boat Harbour during the period of the post-spawning migration and captured at Dillon Bay and Cheyne Beach at the onset of the spawning phase in 1950.

Experiments designed to provide confirmation of the post-spawning migration were not conducted in 1950, but some evidence of the movement was obtained from an operation carried out at Parry's Inlet in March. Of the fish released in this operation, four were recaptured east of the release locality in the period from May to September; a single recapture was obtained at Hopetoun, while three fish were recaptured at Cheyne Beach.

No tagging operations were conducted during the post-spawning period in the years from 1951 to 1953, but in 1954, 51 salmon were released at Eagle Bay in May, and two of these were retaken at Cheyne Beach during the non-spawning phase; the Cheyne Beach and Bremer Bay areas appear to have been within the non-spawning phase habitat in this year. From operations conducted at Parry's Inlet and Cheyne Beach during the pre-spawning migration, three fish were obtained east of the release locality during the period of the post-spawning migration, or during the non-spawning phase; one fish was taken at Cheyne Beach while two were recaptured at Bremer Bay.

It was stated previously that in some years part of the population moves northwards immediately after spawning; schools may be observed in the Perth area in June and July, but it was suggested that these schools subsequently move southwards and eastwards to the non-spawning phase habitat. The northerly movement was confirmed by the recapture of fish at Safety Bay and Bunbury

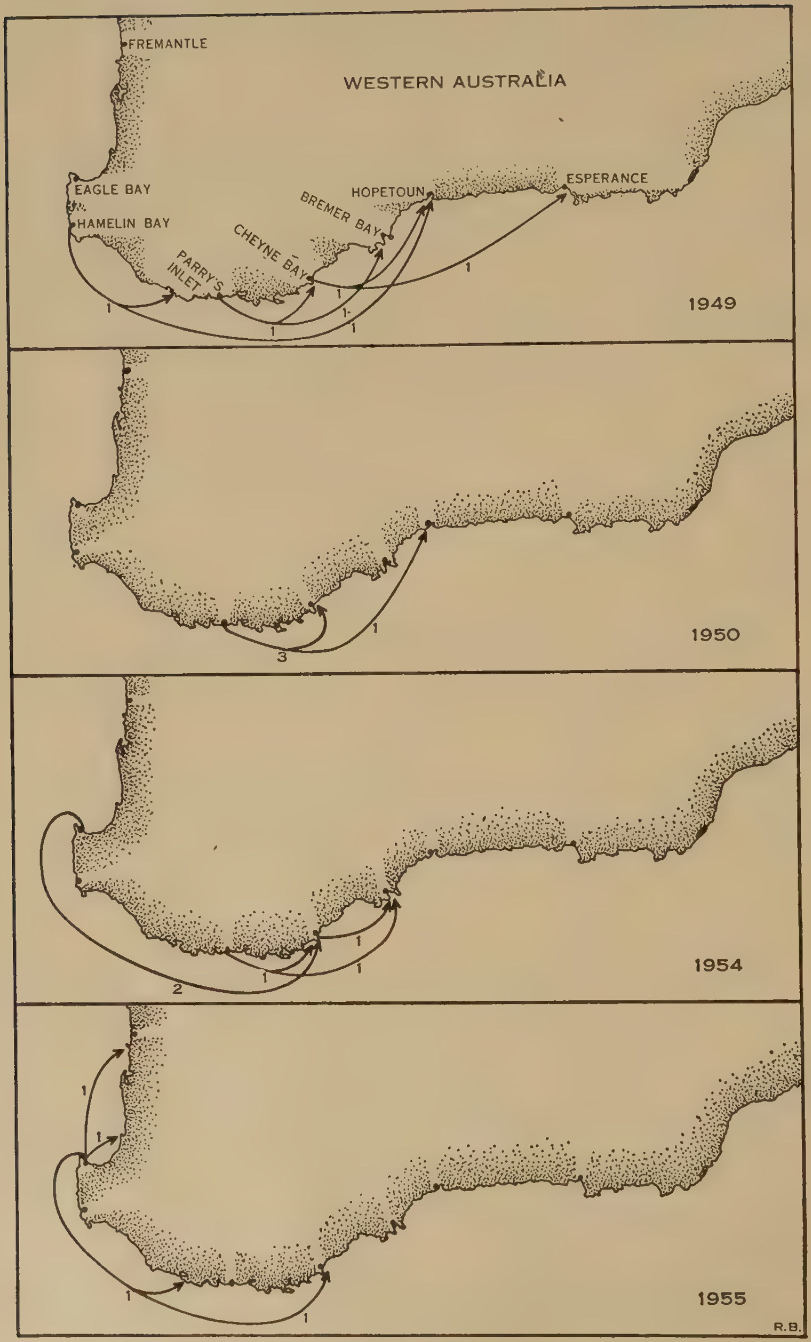
FREMANTLE
WESTERN AUSTRALIA
EAGLE BAY
HAMELIN BAY
PARRY'S INLET
CHEYNE BAY
BREMER BAY
HOPETOUN
ESPERANCE
1
1
1
1
1
1
1949
1
3
1950
1
1
1
2
1954
1
1
1
1
1955
R.B.

Fig. 13.—Post-spawning movements of Australian salmon tagged in Western Australia. The numbers denote the recaptures at each locality.

from a group released at Eagle Bay in May 1955. However, the recovery of an Eagle Bay fish at Cheyne Beach in June indicates that part of the population returned to the southern coast immediately after spawning. It is possible that the fish taken at Chatham Island in September was one that had moved northwards after spawning, and was returning to the southern coast when recaptured.

V. The Use of Age Determination in this Study

The scale reading technique has been used in age determination studies on the Australian salmon. In both subspecies well-defined annuli are generally present in fish up to about 5 years of age, and it is considered that the age determination of these younger fish can be made with a reasonable degree of accuracy. In the older fish the annuli and circuli are no longer clearly deposited, and what appear to be false annuli are invariably present. These scales are difficult to interpret and the ages cannot be determined accurately. It is possible that one annulus or even more could be missed and that the ages of the older fish could be underestimated. Annulus formation occurs normally in October which is the month when minimal environmental temperatures are usually experienced.

A large number of tagging operations have been conducted during the course of these investigations, but these were directed towards the elucidation of the pattern of migration. In some cases, direct evidence of growth was obtained from measurements of individual fish made at release and recapture. In other cases indirect evidence came from the comparison of the size range of the group of fish released and that in which fell most of those recaptured, when the difference in years between the age curves of the released and the recaptured fish corresponded to the years of freedom of the tagged fish. Both categories of evidence corresponded with that from scale reading.

Age data have been used only tentatively in this paper, pending a revaluation of the data already to hand, and a detailed study of age determination and growth. Some error will not affect the general conclusions on the differential distribution of the adults and juveniles and, in view of the results obtained, the use of the age data in predicting the expected time of arrival in Western Australia of the maturing juveniles seems justified.

VI. Discussion

The work reported in the previous sections has led to the following view of the distribution and behaviour of the western subspecies of the Australian salmon. Spawning may take place between the Hopetoun and Busselton areas of Western Australia, but is more likely centred in the Busselton area in April and May. Embryonic, larval, and post-larval life is quite unknown but in this period a drifting, and perhaps later active swimming, eastward must take place to bring the young fish of "0" group to nursery areas in South Australia, western Victoria, and the more westerly regions of Tasmania. Three or four years are spent in these areas during which there are loose local migrations. In the fifth, but more often in the sixth year, the maturing fish move westwards and along the southern coast of Western Australia join, or are joined by, older fish in a migration (pre-spawning) that ends in spawning itself. After spawning, some fish may move northwards; most move back eastwards, but not as far as the nursery areas.

This is a tentative view of the life history, of which certain aspects require closer examination. The position with regard to some of these merits some further discussion at this point.

The evidence provided by the study of the reproductive cycle is the main basis for the conclusion that spawning of the western subspecies salmon is confined to Western Australia, and indeed is centred in the area between Busselton and Cape Leeuwin. Moreover, it is difficult to understand the distribution and movements other than in terms of this conclusion with regard to spawning. But, this being so, since the juveniles inhabit the waters of South Australia, Victoria, and Tasmania, and are found only in small quantities, or exceptionally, in Western Australian waters, it is evident that a movement of the individuals in their early life-history phases must take place from Western Australia to these areas. Nothing is known of this movement, but it probably involves a drift of the eggs and early larvae, supplemented by an active migration of the young fish.

The literature dealing with the current systems operating along the southern coast of Australia is limited, and conclusions that have been drawn are based on few data. Although there is no clear statement on the source regions of the currents, authors agree that the general drift is from west to east (Halligan 1922; David 1932; Schott 1935; British Admiralty 1937). Seasonal westerly sets are recorded in the period from November to January (British Admiralty, loc. cit.) and in February and March (Schott, loc. cit.). The literature is concerned with the major current systems in oceanic areas, and except in the Australia Pilot, consideration is not given to the flow of water on the continental shelf. According to the Australia Pilot, a coastal current, confined to the continental shelf, flows in an easterly direction along the southern coast throughout the year. This current reaches its greatest intensity in the period from May to July. Drift bottle releases by this Laboratory indicate an easterly flow along the southern coast; a bottle released at Albany in May was recovered in eastern South Australia in December. Since April and May appear to be the months of most intense spawning the eggs and larvae are thrown into the system during the period of most intense easterly flow.

Although the initial transport of eggs and larvae would be effected by current, it is inconceivable that the entire movement to the nursery areas could be effected by this means considering that these are warm-temperate waters and that the embryonic phase is unlikely to be of long duration. "0" group fish captured as early as December range from 5 to 10 cm in length; this indicates that the growth of the young fish is comparatively fast. It is possible that the young fish move passively with the current, but it is more likely that in the final stages of these earlier juvenile movements there is an active migration to, or through, water of preferred character.

The evidence provided by distribution of the "0" group and the larger juveniles taken in the commercial catches allows reasonably good definition of the eastern boundaries of the nursery area, but in the absence of data from the area of the Great Australian Bight it is not possible to define the western limits of juvenile distribution. The capture of small fish in the commercial catches at Esperance in 1949, and the presence of the "0" group in the area in that year, suggests that the nursery area may extend into the more easterly areas of Western Australia. However, the absence of the small salmon from the beaches in later years indicates that their appearance in 1949 was atypical, and suggests fluctuations in the boundary of the nursery area. This would not be unexpected if the dispersion of the eggs and larvae involves a denatant movement, or if the distribution of the juveniles is related to a body of water of definite character.

Since there does not appear to be any difference in the general biology of the western subspecies fish inhabiting South Australia, Victoria, and Tasmania, the view is held that the results provided by the more detailed investigation of the South Australian fish can be applied to the fish of the other areas. In general then it can be stated that the juveniles remain in the nursery areas until they approach 5 or 6 years of age, and then migrate to Western Australia for spawning. The absence of reports of a westerly movement of schools along the southern coast of South Australia, and in the Esperance and Hopetoun areas of Western Australia, may be taken to mean that the schools move directly across the Great Australian Bight and do not follow the coastline. By the time these schools reach the south-western corner of Western Australia, and have been joined by the adult fish that have spawned previously and have been distributed in the more easterly areas of Western Australia during the non-spawning period, possibly because of the configuration of the Western Australian coastline, the migration is accomplished by many if not all of the schools in the more inshore waters. This inshore migration provides the basis for the active beach fishery operating between Bremer Bay and Busselton. This migration may be compared with that reported by Sette (1950) for the Atlantic mackerel, *Scomber scombrus* L., which commences to migrate well offshore, but whose later stages of movement are confined to the inner half or third of the continental shelf waters.

After spawning some schools may penetrate north to the Perth area, but most schools return to the southern coast of Western Australia. The small number of schools observed moving along the beaches in post-spawning migration suggests that many schools accomplish this movement in more seaward waters. The easterly limit of the adult distribution area is not known, nor can the life span of the fish be stated. The largest fish measured was 80 cm and, in the light of the age determination study so far conducted, would be 9 or more years of age.

The account given here is of the distribution and movements of the salmon which have been deduced from a limited range of evidence. These limits, imposed by the nature of the fishery and the restrictions placed on the research workers, have meant that this had to be confined to an account of coastal distribution and movement. There is direct evidence of at least some movement into and through deeper water. Bass Strait is traversed by some migrants, and as the organisms on which the salmon feeds live away from the beaches, the fish must move to sea to feed. Since it is most likely that spawning also takes place out to sea, the presence of the salmon on the beaches is a little difficult to understand. It is still more difficult to guess whether all salmon move on to the beaches since such movement does not appear essential to spawning or feeding. It is possible that only a proportion of the total stock moves inshore or, more likely, that each fish (or school) spends only a proportion of its time inshore. It would follow that the fishery operates on only a proportion of the stock, and further work must be done to measure this proportion. Finally, it must be noted that if the foregoing is true, there is a possibility that the fishery in the Busselton area operates on a lower proportion of the stock than the other main fishing areas, because of the concentration of the schools on the spawning area away from the coast.

Certain features of this account require further investigation. Thus, it is obviously desirable to know more about the spawning area, and the early embryonic and larval history. Other matters requiring elucidation are the spermatogenic development in non-migratory males and the differential ovarian and testicular development in South Australia. Again, the migration from Victoria and Tasmania to Western Australia, and the relationship of distribution and migration to the environment must be studied more closely. However, the major undetermined features are the total area of distribution and the size of the total stock.

VII. Acknowledgments

The author wishes to thank Professor H. Waring of the University of Western Australia for providing laboratory facilities in the Department of Zoology during the course of these investigations. Valuable assistance in the tagging studies has been given by Mr. A. J. Fraser, Director, and various officers, particularly Mr. L. G. Smith, of the Fisheries and Game Department of Western Australia.

Prior to 1949 salmon tagging studies in Western Australia were the responsibility of Dr. D. L. Serventy, Wildlife Survey Section, C.S.I.R.O., then of the Division of Fisheries, who has kindly given the author access to unpublished data.

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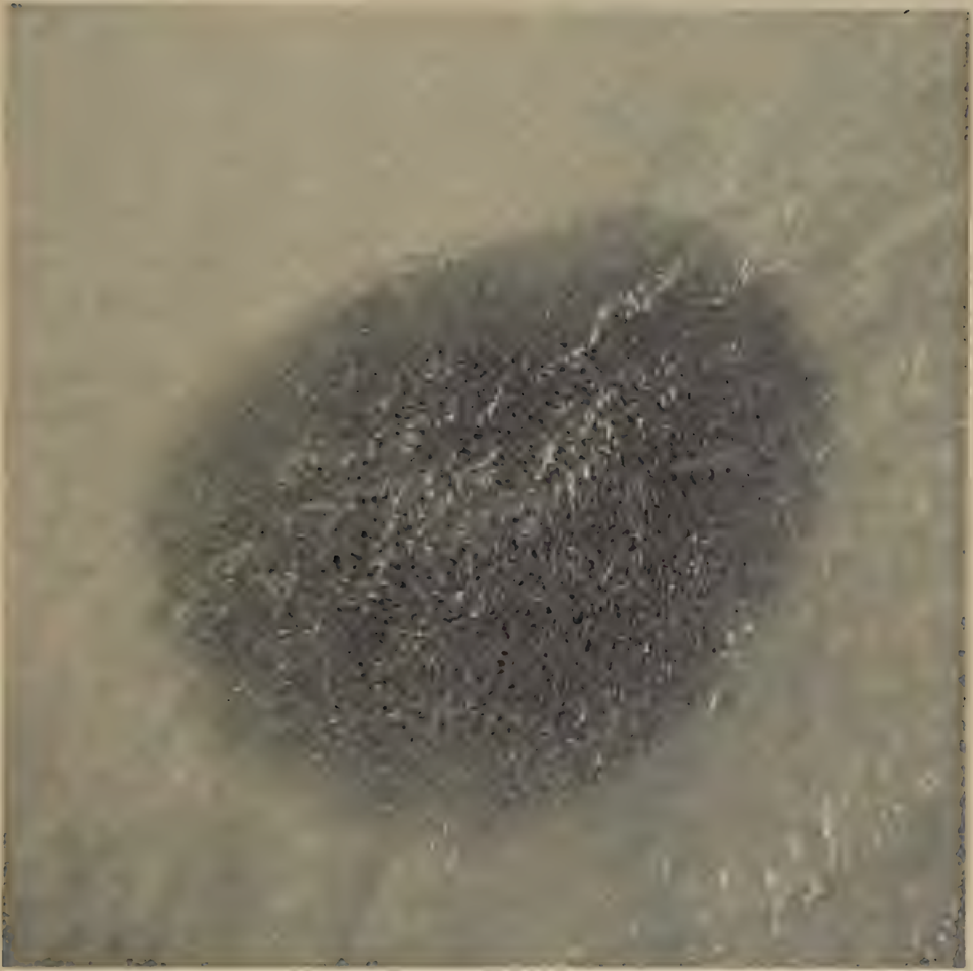
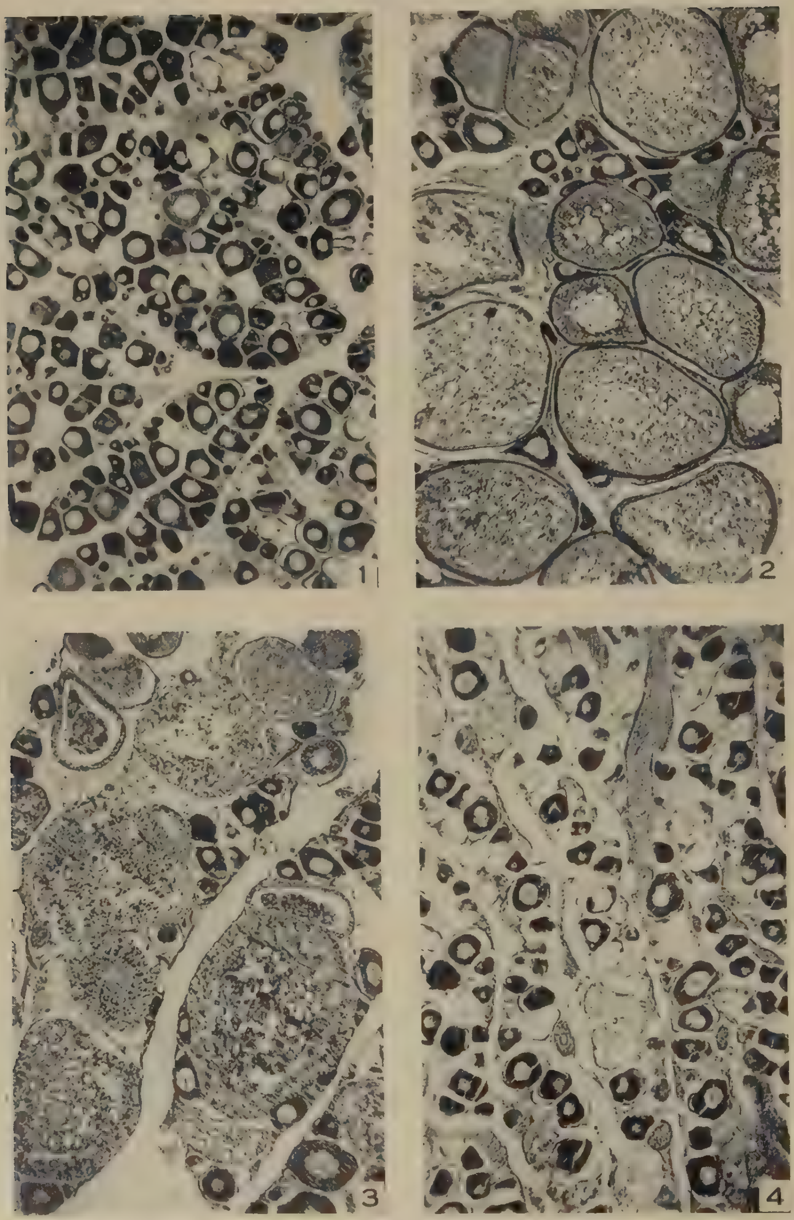


Aerial photograph of salmon in shallow coastal waters. The individual fish approximate 5 lb in weight. (Photograph by S. Fowler.)



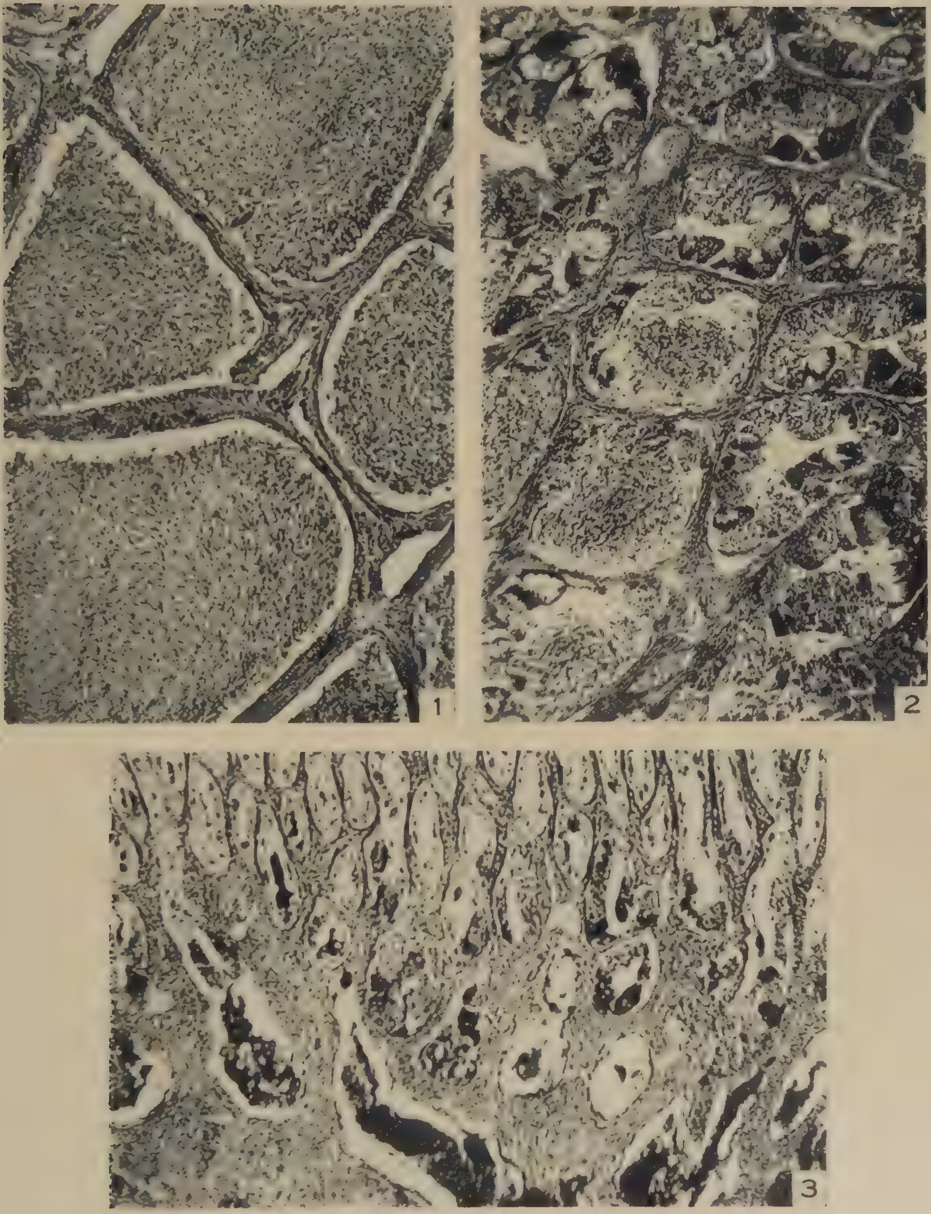
Sections of ovaries from western subspecies taken in Western Australia. ×100

Fig. 1.—During the non-spawning phase.

Fig. 2.—Showing active pre-spawning development.

Fig. 3.—Showing commencement of post-spawning degeneration and resorption.

Fig. 4.—Showing completion of post-spawning degeneration and resorption.



Sections of testes from western subspecies. ×140

Fig. 1.—From Western Australia, showing enlarged tubules occupied by spermatozoa.
Fig. 2.—From South Australia, showing active spermatogenesis.
Fig. 3.—From South Australia, showing degeneration of spermatogenic products.

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AN ANALYSIS OF VARIATION IN AUSTRALIAN SPECIMENS OF *PINCTADA ALBINA* (LAMARCK) (LAMELLIBRANCHIA)

By J. S. Hynd*

[*Manuscript received April* 14, 1960]

Summary

An analysis is made of variation in Australian specimens of *Pinctada albina* (Lamarck). Eight characters are investigated, and it is shown that these characters fall into two well-defined and unrelated groups.

In one group lie those characters which modify shape of shell. They are shown to vary with ecological conditions but not geographically.

In the other group lie those characters which modify colour and size of shell. Their variations are not ecological but are interpreted as geographical discontinuities, or clines, dividing the species into eastern and western subspecies.

Shark Bay is selected as designated typical locality for *Pinctada albina* (Lamarck); and *P. albina albina* (Lamarck) and *P. a. sugillata* (Reeve) respectively are the valid names for the western and eastern subspecies.

I. Introduction

In an earlier paper on the Australian pearl-shells (Hynd 1955) two subspecies of *Pinctada albina* (Lamarck) were recorded, one from Shark Bay, Western Australia, and the other from Northern Territory, Queensland, and New South Wales. The western subspecies is lightly pigmented, the eastern more heavily so, but there are intergrading populations and the range of variation within populations is considerable.

In the present paper an attempt is made to determine the relative importance of geographic location, ecological conditions, and age in modifying the specific characters. Further, the nature of the relationship between the two subspecies is investigated.

Throughout this paper certain variations in the selected characters are referred to as geographic. This term is used to indicate a trend or cline coastwise from west to east (or vice versa) throughout the range of the species along the northern Australian coast. These variations are assumed to be genotypic because no ecological factors forming a gradient coastwise were observed, and it is difficult to envisage such a factor varying in this way over the known range of the species. Geographic isolating mechanisms have not been demonstrated, but they are assumed to exist and the clines are referred to as geographic in distinction to the ecological variations due to type of niche, which do not show as a geographic cline.

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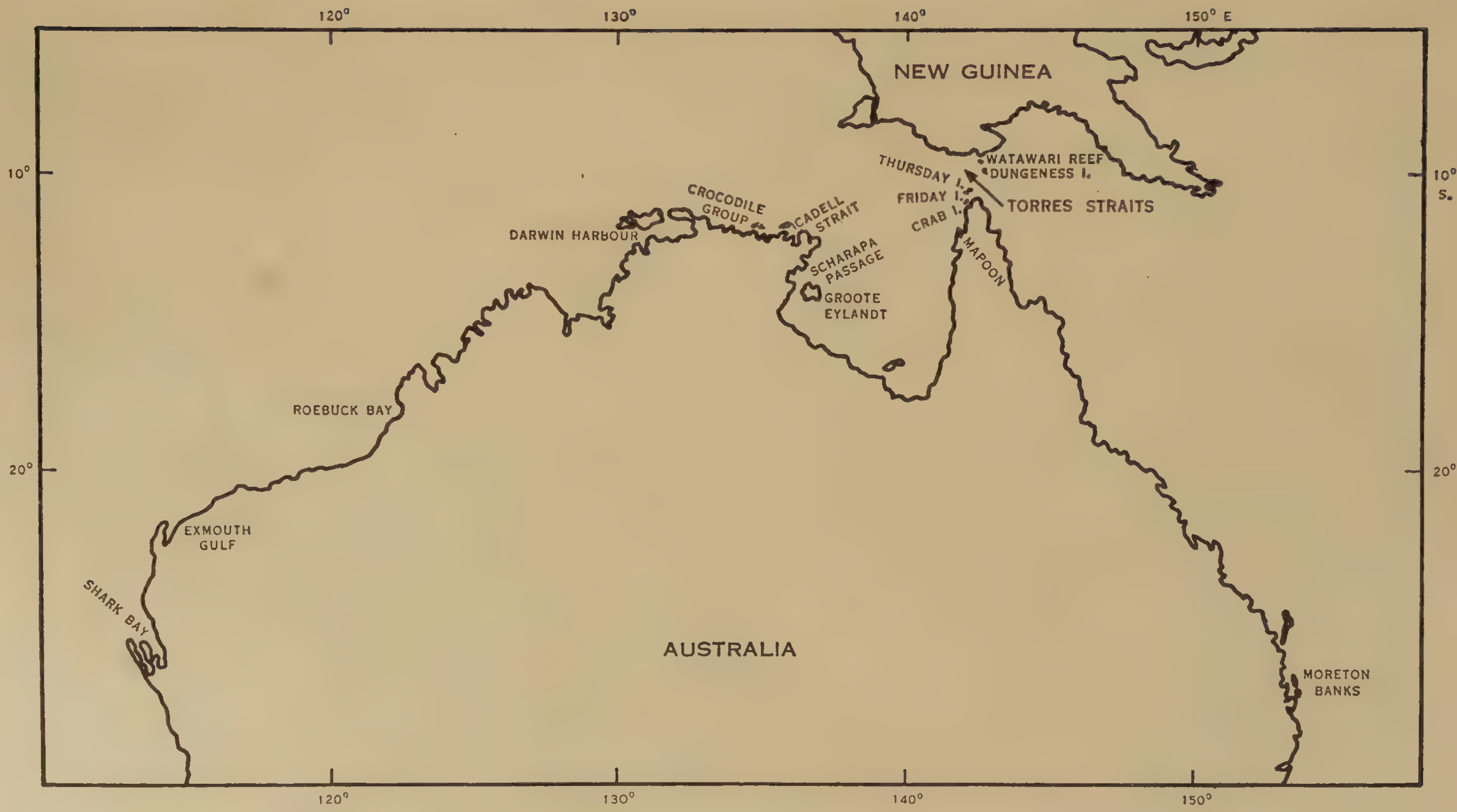
120°
130°
140°
150° E
10°
10° S.
20°
20°
NEW GUINEA
WATAWARI REEF
DUNGENESS I.
THURSDAY I.
FRIDAY I.
CRAB I.
TORRES STRAITS
MAPOON
CROCODILE GROUP
CADELL STRAIT
SCHARAPA PASSAGE
GROOTE EYLANDT
DARWIN HARBOUR
ROEBUCK BAY
EXMOUTH GULF
SHARK BAY
AUSTRALIA
MORETON BANKS
120°
130°
140°
150°

Fig. 1.—Northern coast of Australia, showing localities at which samples were collected.

II. Materials and Methods

The area sampled extends from Shark Bay in Western Australia, along the northern coast of the continent, and down the east coast of Queensland to Moreton Bay. Three specimens from Leighton, Western Australia, were also examined. The localities where specimens were collected are shown in Figure 1.

Sixteen samples containing 3499 specimens were obtained. In only one sample were numbers less than 100, and the samples were generally more than 200. Details of samples, including dates of collection, are given in Table 1. The samples were collected during the years 1949 to 1956. In some cases the whole sample was col-

Table 1

LIST OF SAMPLES WITH ECOLOGICAL DETAILS

Samples	Geographical Rank		
	All Samples	Omitting Deep Water Samples	Omitting Deep Water and Harbour Samples
INTERTIDAL SAMPLES			
Shark Bay, W.A. 228 specimens from just below intertidal zone on a sandy bottom. October 1955	1	1	1
Exmouth Gulf, W.A. 118 specimens from intertidal reef. September 1953	2	2	2
Roebuck Bay, W.A. 157 specimens attached to rocks in middle portion of intertidal zone at Quarantine Point. July 1954	3	3	3
Darwin Harbour, N.T. 119 specimens from wharf piles at bottom of intertidal zone. October 1954 and October 1956	4	4	
Cadell Strait, near Elcho Island, N.T. 480 specimens from outcropping rocks on mudflat at bottom of intertidal zone. October 1953 and December 1954	6	5	4
Scharapa Passage, Groote Eylandt, N.T. 191 specimens attached to razor shells etc. or lying in clumps on *Posidonia* covered mudflat at bottom of intertidal zone. July, November, December 1952	7	6	5
Mapoon, Gulf of Carpentaria, Qld. 122 specimens attached to rocks etc. of reef outside Batavia River mouth in lower half of intertidal zone. June, December 1952	9	7	6
Crab Island, Gulf of Carpentaria, Qld. 364 specimens from mainland coast behind Crab Island, attached to razor shells etc. on mudflat at bottom of intertidal zone. June, October 1953	12½	10	8½

TABLE 1 (*Continued*)

Samples	Geographical Rank		
	All Samples	Omitting Deep Water Samples	Omitting Deep Water and Harbour Samples
Friday Island, Torres Strait, Qld. 100 specimens from outcropping rock on exposed sandbank to west of Friday Island in lower half of intertidal zone. August 1952, May 1953	12½	10	8½
Thursday Island Harbour, Torres Strait, Qld. 585 specimens off wharf piles at bottom of intertidal zone. Monthly samples from August 1952 to September 1953	12½	10	
Dungeness Island, Torres Strait, Qld. 232 specimens from outcropping rocks on reef flat in lower half of intertidal zone. July 1953	12½	10	8½
Watawari Reef, Torres Strait, Qld. 139 specimens attached to razor shells etc., on reef flat in lower half of intertidal zone. July 1953	12½	10	8½
Moreton Banks, Moreton Bay, Qld. 208 specimens attached to razor shells etc. on *Zostera* flat at bottom of intertidal zone. August 1949, September 1951	16	13	11
DEEP WATER SAMPLES			
Torres Strait, Qld. 151 specimens from various localities in depths of 8–16 fm. October 1949, December 1953, October 1954, May 1955	12½		
Groote Eylandt, N. T. 269 specimens from various localities between Groote Eylandt and Arnhem Land in depths of 8–12 fm. December 1952, November 1953, November 1954	8		
Crocodile Group, N.T. 36 specimens from various localities in the Crocodile Group in depths of 12–20 fm. November 1954	5		

lected at the one time, in others the sample was the result of pooling two or more collections. The possibility of changes in the populations from year to year has been ignored in the analysis. The samples were grouped on ecological grounds into "intertidal samples", which were taken at, or near, low water springs, and "deep water samples", which were taken by divers in depths ranging from 8 to 20 fm.

Eight separate characters have been investigated, only one of which, dorso-ventral measurement–heel depth relationship (see Hynd (1955) for explanation of these and subsequent terms), was quantitative. For statistical analysis a method was devised to express the qualitative characters numerically. Where degree of development of a character was concerned, a specimen in which the character showed maximum development was selected as a standard and this was rated as +++.

Intermediate stages were selected to represent the + and ++ degrees of development. Thus the degree of development in any particular specimen could be determined by comparison with the standards and be expressed as either 0, +, ++, or +++. To express the degree of development in a sample, the number of specimens with a +++ classification was multiplied by 3, the number of specimens with a ++ classification by 2, the number of specimens with a + classification by 1, and the figures so obtained were added and expressed as a percentage of the numbers in the sample. In actual practice the samples were divided into centimetre class intervals of dorsoventral measurement (D.V.M.) and millimetre class intervals of heel depth before this "scoring". As a result a score was obtained for each class interval. These scores were tabulated but the resultant tables were too voluminous to reproduce. Instead the results have been expressed graphically. The details of the method can be seen in Table 2.

The characters treated thus were projection of anterior border, projection of posterior ear, projection of posteroventral border, yellow nacre, and black band distal to nacre.

The remaining two qualitative characters could not be expressed by this method. Colour pattern was expresssed as one of the three alternatives, rayed, dark, or light; and form of shell was expressed as either oblique, erect, or obtuse. Again, tables were constructed using centimetre class intervals of D.V.M. and millimetre class intervals of heel depth in each sample, but the samples were not scored as for the other characters. Instead the number having a particular attribute was expressed as a percentage of the class interval to which it belonged. Histograms were prepared for each character.

All samples were handled by two observers: one who numbered, measured, and recorded all specimens, and another who checked the measurements and recordings. Where there was any disagreement between the two assessments, it was settled by discussion.

Two of the mathematical processes employed in the analyses require some explanation. In testing for correlations between development of characters and geographical position or ecological conditions, rank correlations have been used. This was unavoidable as it was impossible to classify the various ecological categories more accurately than by ranking. Kendall's rank correlation method (Kendall 1948) was employed in preference to Spearman's, as partial correlations are involved and the theory of partial Spearman rank correlation coefficients has not yet been evolved.

In testing for associations between characters, contingency tables have been employed. Where three numbers occur in each cell the upper is the observed frequency, the middle is the expected frequency, and the lower is the difference. Where four numbers occur in each cell the upper is the observed frequency, the next is the observed frequency expressed as a percentage of a border frequency, the next is the expected frequency, and the lower is the difference. χ^2 tests have been employed to determine the significance or otherwise of the differences.

Table 2

PROJECTION OF ANTERIOR BORDER; FREQUENCIES OF FOUR CLASSES AND SCORE IN EACH OF THE FIRST SIX SAMPLES TABULATED IN CM CLASS INTERVALS OF D.V.M.

Sample	Classification and Scoring	D.V.M., cm Class Intervals										Totals
		0–1·0	1·1–2·0	2·1–3·0	3·1–4·0	4·1–5·0	5·1–6·0	6·1–7·0	7·1–8·0	8·1–9·0	>9·0	
Shark Bay	0		1	16	10	2	1	13	56	80	36	215
	+					1		1	1	5	4	12
	++									1		1
	+++											
	Totals		1	16	10	3	1	14	57	86	40	228
	Score		0	0	0	33	0	7	2	8	10	
Exmouth Gulf	0	16	74	6	3	5	3	1	1			109
	+				2				1			3
	++						3	1	1			5
	+++							1				1
	Totals	16	74	6	5	5	6	3	3			118
	Score	0	0	0	40	0	100	167	100			
Roebuck Bay	0		20	26	12	12	10	20	14	6	3	123
	+			3	6	5	3	3	4	1	2	27
	++		1	1	1	1	2		1			7
	+++											
	Totals		21	30	19	18	15	23	19	7	5	157
	Score		10	17	42	39	47	13	32	14	40	
Darwin Harbour	0			1	3	6	5	1	5	4		25
	+			1	13	5	5	9	7	6	2	48
	++				2	2	5	6	8	10	3	36
	+++						3		3	2	2	10
	Totals			2	18	13	18	16	23	22	7	119
	Score			50	94	69	133	131	139	145	200	
Cadell Strait	0		12	56	81	91	97	63	21	6		427
	+		2	4	21	14	7	4				52
	++						1					1
	+++											
	Totals		14	60	102	105	105	67	21	6		480
	Score		14	7	21	13	9	6	0	0		
Scharapa Passage	0	20	32	30	20	9	17	27	26	1		182
	+		2	3		1	2	1				9
	++											
	+++											
	Totals	20	34	33	20	10	19	28	26	1		191
	Score	0	6	9	0	10	11	4	0	0		

III. ANALYSIS

(*a*) *General*

The magnitude of the changes with age that take place in pearl-shells has already been stressed by Hynd (1955). Almost every one of the taxonomic characters described was found to be subject to considerable changes. Unfortunately there is no intrinsic evidence of age in individuals* other than size. Accordingly two measurements, D.V.M. and heel depth, were selected as representative of size, and the data tabulated in centimetre class intervals of D.V.M. and millimetre class intervals of heel depth.

However, no attempt is made to attribute a definite age to any class interval because during spat collecting and shell culture work it has been found that there are considerable variations in both these measurements among individuals of the same age. Tranter (1958*b*, Fig. 5*c*) gives a frequency histogram of the D.V.M. of young *P. albina* all approximately of the same age. Inspection shows considerable variation. Measurements of the same specimens taken for this author gave a range of D.V.M. from 2·3 to 7·7 cm and of heel depths from 0·5 to 2·0 mm. Thus neither measurement forms a suitable basis for age determination. The diversity in growth rates in this case was due to overcrowding (cf. Crossland's results with overcrowded spat of *P. margaritifera* (Crossland 1957, p. 121)). Specimens growing under natural conditions may not show such a diversity in growth rates, as overcrowding to the same extent rarely occurs. However, differences do occur, and consequently neither measurement can be used as an accurate measure of age.

The class intervals of D.V.M. do not correspond to equal time intervals. Tranter (1958*a*, p. 141, Table 1) gives the D.V.M. and heel depths of the largest oysters from a number of samples of known age. When these measurements are plotted against age it is found that the D.V.M.–age relationship is approximately exponential while the heel depth–age relationship is approximately linear. (Malpas (1933) obtained similar results with *P. fucata* (Gould) in Ceylon.) Thus the class intervals of heel depth represent approximately equal time intervals but the lower class intervals of D.V.M. represent relatively shorter time intervals than the higher ones.

(*b*) *D.V.M.–Heel Depth Relationship*

Various authors (Nomura 1926; Soot-Ryen 1927; Hamai 1934*a*, 1934*b*, 1936, 1938; Orton 1935; Newcombe 1936; Newcombe and Kessler 1936; Newcombe, Thompson, and Kessler 1938; Fox and Coe 1943) have shown that examination of relative growth rates of bivalve molluscs may reveal genotypic or phenotypic variations. The D.V.M.–heel depth relationship was selected for investigation in this species.

Scatter diagrams were prepared for each sample on linear graph paper and smooth curves fitted by eye. The curves were then superimposed. It was seen that they were all of approximately exponential form but there was quite a spread in their distribution and some crossing. Also in those samples which contained adequate numbers of specimens with large heel depths the curves were approaching or had reached a finite limit of D.V.M. Some of these curves are shown in Figure 2.

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* Sagara and Takemura (1960) have recently demonstrated the presence of growth rings in *Pinctada maxima*.

It was found that if D.V.M. were plotted against log (heel depth) the data could be represented adequately by a straight line within the range of heel depths 1 to 6 mm inclusive. Thus it is convenient to consider the data in two sections: from 1 to 6 mm heel depth, and over 6 mm heel depth. The first section contains the young and middle-aged specimens, the second section contains old and senile specimens. In the section containing specimens of over 6 mm heel depth only two samples, Shark Bay and Scharapa Passage, contained sufficient specimens to allow maximum D.V.M. to be estimated. Under these circumstances no analysis was attempted.

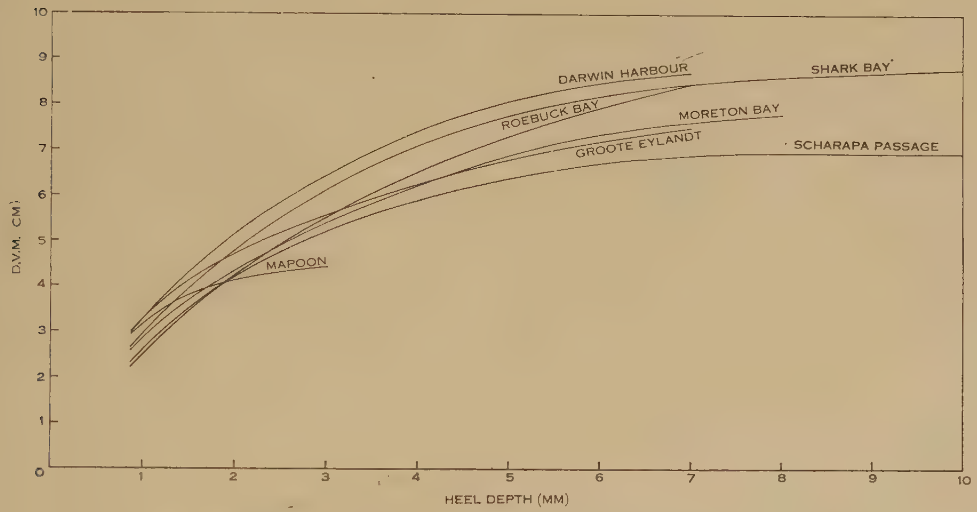

Fig. 2.—*Pinctada albina* (Lamarck). D.V.M.–heel depth curves for selected samples.

In the first section, comparisons were made between straight lines fitted by the least squares method. The lines were of the form

$$\log (\text{heel depth}) = a + b \times (\text{D.V.M.}).$$

The resultant values of b and their standard deviations are given in Table 3.

Inspection shows that there is pronounced grouping. There is a western intertidal group composed of the Shark Bay, Exmouth Gulf, and Roebuck Bay samples with high values of b. There is an eastern intertidal group composed of all samples from Cadell Strait to Moreton Banks in which the values of b are of the same order (except the Mapoon sample) and lower than those of the western group.

The value of b of the Darwin Harbour sample is intermediate. The values of b of the deep water samples show considerable variation, in fact the range of values of b is comparable to that of the intertidal samples if the Mapoon sample is left out of account. This indicates that a much larger range of samples would be necessary for an effective analysis and accordingly no analysis was attempted.

F and t tests were carried out on the values of b. No significant differences could be demonstrated within the western group ($F<1$, therefore not significant) or the eastern group, excluding the Mapoon sample ($F<1$, therefore not significant). However, the difference between the means of the two groups was significant ($F = 24\cdot38$ on 1 and 50 degrees of freedom, $P\ll0\cdot001$). The Darwin Harbour sample did not differ significantly from either the western or eastern group ($t = 1\cdot79$ on 50 degrees of freedom, $0\cdot05<P<0\cdot10$; $t = 1\cdot43$ on 50 degrees of freedom, $0\cdot10<P<0\cdot20$ respectively). These results are illustrated graphically in Figure 3 where the values of b are plotted against the easterly distance from Shark Bay.

TABLE 3

D.V.M.–HEEL DEPTH RELATIONSHIP

Constants of log (heel depth) $= a+b\times$(D.V.M.) fitted to data of each sample

Sample	b	Standard Deviation of b	a Calculated Using Mean b for Western Group	a Calculated Using Mean b for Eastern Group	Remaining a Values	Rankings by a Values within Eastern Group
Shark Bay	8·08	0·585	2·19			
Exmouth Gulf	8·33	0·832	1·74			
Roebuck Bay	7·91	0·585	1·86			
Darwin Harbour	6·82	0·585			3·35	
Cadell Strait	5·43	0·585		2·42		5
Scharapa Passage	6·15	0·585		2·22		7
Mapoon	2·64	1·105			3·29	
Crab I.	5·72	0·832		2·61		4
Friday I.	5·75	0·585		1·96		8
Thursday I. Harbour	6·29	0·585		3·39		1
Dungeness I.	5·79	0·585		2·32		6
Watawari Reef	6·19	0·832		2·65		3
Moreton Banks	6·15	0·585		2·73		2
Torres Strait	7·31	0·585			2·75	
Groote Eylandt	4·88	0·585			3·28	
Crocodile Group	6·45	1·264			2·77	

The low value of b for the Mapoon sample is significantly different ($t = 2\cdot93$ on 50 degrees of freedom, $0\cdot001<P<0\cdot01$) from the remainder of the eastern group. It is also possible to demonstrate other differences within this group. The values of a for each sample in the group were calculated using a mean value of b. They are also listed in Table 3. An F test (omitting the Mapoon sample) showed that the observed differences were significant ($F = 2\cdot91$ on 6 and 50 degrees of freedom, $0\cdot01<P<0\cdot05$).

There was no geographical trend from west to east within the group because the rank correlation coefficient between the samples ranked according to their values of a (Table 3) and geographically (Table 1), was $0\cdot36$ ($P = 0\cdot32$).

The values of a for the three western group samples are also given in Table 3. The observed difference was not significant ($F = 2 \cdot 03$ on 2 and 50 degrees of freedom, $0 \cdot 10 < P < 0 \cdot 20$).

It has now been shown that in young to middle-aged specimens there is a pronounced geographical grouping in the D.V.M.–heel depth relationship such that

(1) the higher ratios of D.V.M. to heel depth are found in the northern part of Western Australia, and the lower ratios in the eastern part of Northern Territory and Queensland;

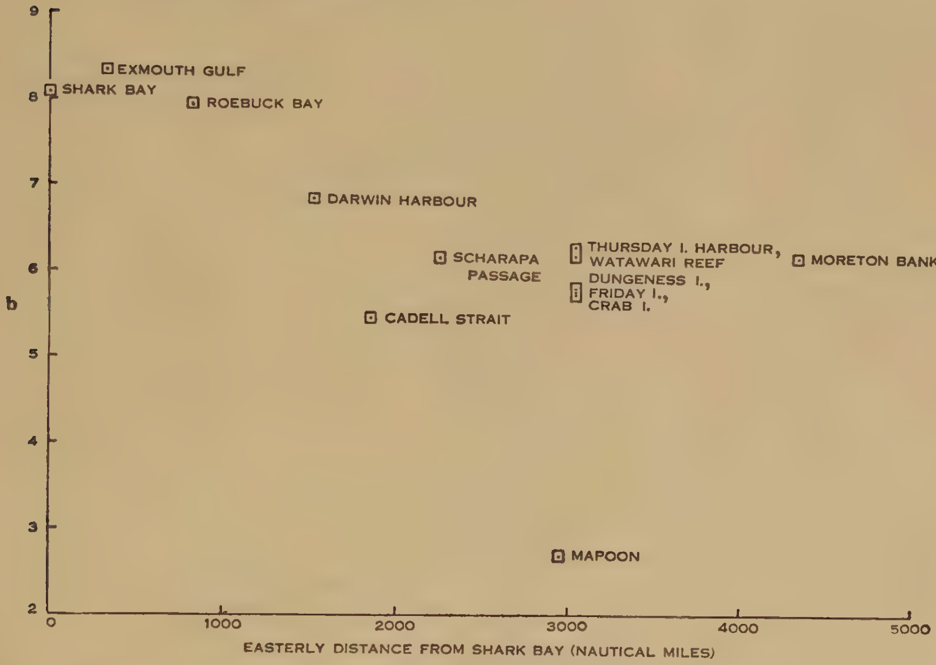

Fig. 3.—*Pinctada albina* (Lamarck). D.V.M.–heel depth relationship. Value of b for intertidal samples plotted against easterly distance from Shark Bay.

(2) intragroup variation was demonstrated in the eastern group though not in the western group and this variation does not appear to be of a geographical nature. It is possible that this variation is the result of an ecological condition, but during these investigations, no condition that might affect growth rates and could be easily measured or otherwise expressed suggested itself, so no further inferences can be drawn.

(c) *Projection of Anterior Border*

The general nature of the changes in the anterior border and the use of the "reference line" as a criterion of development have been described and figured by Hynd (1955). In very young specimens, which are oblique, the anterior border lies behind the reference line (Hynd 1955, Plate 9, Fig. 3). In older specimens, most of which are erect, the anterior border lies well in advance of the reference line

(Hynd 1955, Plate 10, Figs. 1, 2; Plate 11, Fig. 3; Plate 12, Fig. 3). This is regarded herein as the normal or 0 classification. However, in some specimens (e.g. Hynd 1955, Plate 10, Fig. 3) the anterior border projects much further than this. The specimen in Plate 10, Figure 3, rates ++ while the specimen in Plate 11, Figure 2, rates +. The +++ condition is seen in Plate 1, Figure 1, in this paper.

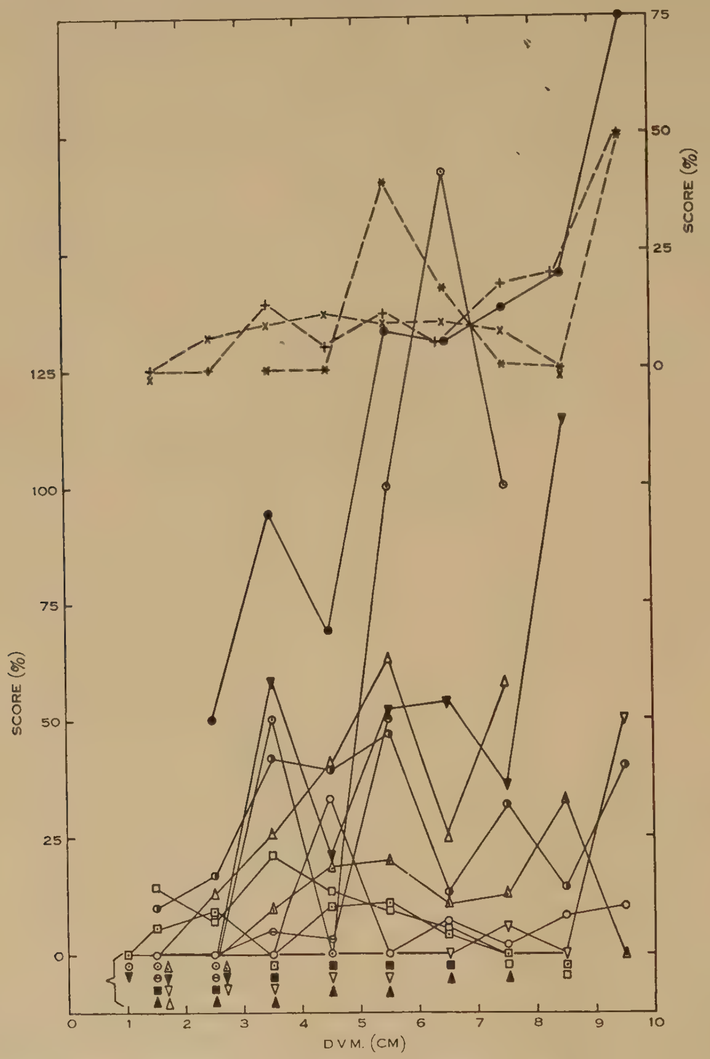

Fig. 4.—*Pinctada albina* (Lamarck). Projection of anterior border. Score plotted against D.V.M. for 16 samples.

○ Shark Bay
□ Cadell Strait
△ Friday I.
▽ Moreton Banks
⊙ Exmouth Gulf
⊡ Scharapa Passage
◬ Thursday I. Harbour
+ Torres Strait
◑ Roebuck Bay
⊖ Mapoon
▼ Dungeness I.
× Groote Eylandt
● Darwin Harbour
■ Crab I.
▲ Watawari Reef
★ Crocodile Group

- - - - deep water samples
——— intertidal samples

The samples have been scored as described above and the data plotted (Figs. 4 and 5). The data from intertidal and deep water samples have been presented separately in these and subsequent figures. All the intertidal samples with the exception of Crab Island and Watawari Reef contain some specimens in which the character is well developed. There is no appreciable development below 2 cm D.V.M. or 1 mm heel depth. After 2 cm D.V.M. or 1 mm heel depth, development is variable, but in most of the samples increasing continuously, though the Cadell Strait sample increases at first then decreases. The extreme jaggedness of the

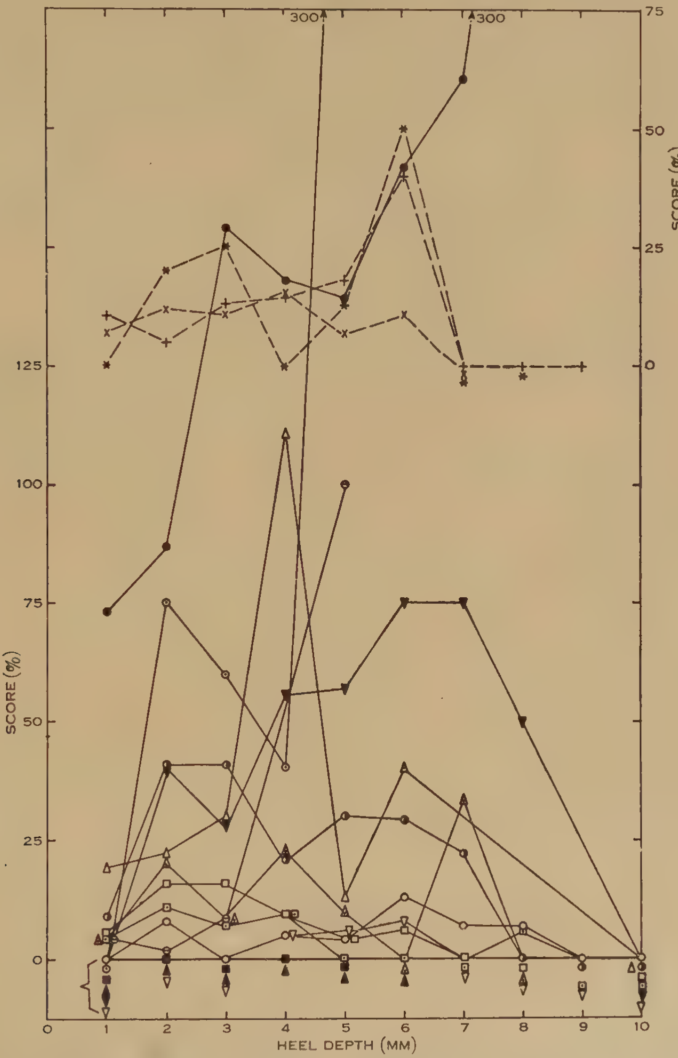

Fig. 5.—*Pinctada albina* (Lamarck). Projection of anterior border. Score plotted against heel depth for 16 samples. For meaning of symbols see Figure 4.

graphs in the higher D.V.M.'s and heel depths is due to the small numbers of specimens in the class intervals.

A mean score for each sample was calculated by averaging the score for each class interval. This was done for both D.V.M. and heel depth tables and the means of the pairs of means from each sample are listed in Table 4 in descending order of magnitude. The rank correlation coefficient between this ranking and the samples ranked from west to east is 0·24 ($P = 0{\cdot}23$). Omitting the deep water and harbour samples the correlation coefficient is 0·25 ($P = 0{\cdot}30$).

TABLE 4

PROJECTION OF ANTERIOR BORDER: MEAN SCORES AND RANKS FOR ALL SAMPLES

Samples	Mean Score (%)	Rank		
		All Samples	Omitting Deep Water Samples	Omitting Deep Water and Harbour Samples
Darwin Harbour	140	1	1	
Exmouth Gulf	86	2	2	1
Dungeness I.	43	3	3	2
Friday I.	33	4	4	3
Roebuck Bay	24	5	5	4
Mapoon	21	6	6	5
Crocodile Group	15	7		
Torres Strait	13	8		
Thursday I. Harbour	12	9	7	
Groote Eylandt	8·1	10		
Cadell Strait	8	11	8	6
Shark Bay	6	12	9	7
Scharapa Passage	5	13	10	8
Moreton Banks	4	14	11	9
Watawari Reef	0	15	12	10
Crab I.	0	16	13	11

Anterior border tends to be well developed in specimens growing on or under flat rock slabs or in cracks in rocks (Hynd 1955). The intertidal samples are ranked in Table 5 according to the quantity of flat or cracked rocks in the locality. The samples at the lower end of the list are from localities which contained no rocks. They were flat, sandy, or grassy banks. Darwin Harbour and Thursday Island Harbour samples were omitted as they were not amenable to such classification. The rank correlation coefficient between this ranking and the samples as listed in Table 4 is 0·74 ($P = 0{\cdot}003$) indicating a moderately strong correlation between well-developed projection of the anterior border and a rock environment, significant at the 1 per cent. level.

In addition, the rank correlation between the samples listed in Tables 1 and 5 was found to be 0·15 ($P = 0{\cdot}61$). Therefore there does not appear to be any relationship between the location of the samples and the amount of rocks in the environment from which they were taken, hence the possibility of an illusory correlation between projection of anterior border and rocky environment is eliminated.

From these three coefficients the partial correlation coefficient of anterior border with rocky environment excluding geographical position was found to be 0·74. Therefore development of anterior border is moderately strongly associated with a rocky environment.

TABLE 5

INTERTIDAL SAMPLES* RANKED ACCORDING TO THE AMOUNT OF ROCKS IN THE ENVIRONMENT

Sample	Rank
Friday Island—entirely rocky	1
Roebuck Bay	2
Exmouth Gulf	3
Dungeness Island	4
Mapoon	5
Cadell Strait	6
Watawari Reef—no rocks	9
Scharapa Passage—no rocks	9
Crab Island—no rocks	9
Shark Bay—no rocks	9
Moreton Banks—no rocks	9

* The two harbour samples are omitted.

Inspection of the scores for the harbour samples shows that although Darwin has the highest score of all samples, Thursday Island has a relatively low one. No explanation is apparent. The scores for the deep water samples are all low and are of the same order of magnitude as those for samples from intertidal non-rocky environments probably because the bottoms contained very few rocks.

(*d*) *Projection of Posterior Ear*

The general outline of the changes in the projection of the posterior ear have been described by Hynd (1955) and illustrated in the following plates and figures: There is never a posterior ear in very young specimens (e.g. Plate 9, Fig. 3), thereafter development is variable, usually increasing for a while, but almost always falling away again with increasing age; up to 70 per cent. of young specimens may show this character. The specimens shown in Plate 11, Figures 1, 3, and Plate 12, Figures 1, 2, 3 (loc. cit.), are all examples of the 0 condition. The specimens in Plate 10, Figure 2, and Plate 11, Figure 2, illustrate the + condition and those in Plate 10, Figures 1, 3 (loc. cit.), illustrate the ++ condition. The +++ condition is seen in the present paper in Plate 1, Figure 2.

The samples have been scored as described above and the data plotted. Figures 6 and 7 show that, with a few exceptions, development of the character reaches a maximum between 1 and 4 cm D.V.M. and usually between 2 and 3 cm D.V.M. or between 1 and 3 mm heel depth. Thereafter there is a progressive decrease. The results from Shark Bay, Exmouth Gulf, and Crocodile Group samples in which the maxima are located above 4 cm D.V.M. and 3 mm heel depth do not conform to this pattern. The jaggedness of some of the curves (Figs. 6 and 7) in the higher D.V.M.'s and heel depths is due to the small numbers of specimens in the class intervals.

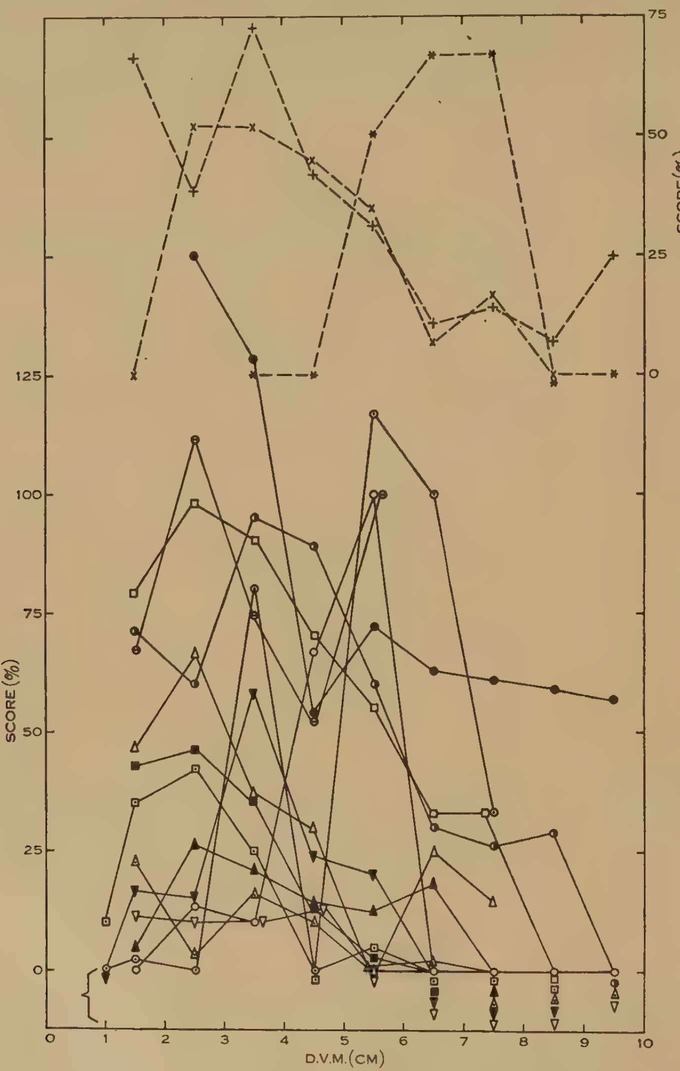

Fig. 6.—*Pinctada albina* (Lamarck). Projection of posterior ear. Score plotted against D.V.M. for 16 samples. For meaning of symbols see Figure 4.

The differences observed in the heights of the peaks are significant and can be readily analysed. In Table 6 the samples are listed in descending order of the height of their peaks in Figures 6 and 7, except that the high values of the Shark Bay sample in the 4–6 cm range have been neglected. Rank correlation coefficients between these rankings and the samples ranked geographically have been calculated. When all samples are included the coefficients are 0·37 ($P = 0·06$) and 0·44 ($P = 0·03$) for the D.V.M. and heel depth ranking respectively. Omitting the deep water and harbour samples the corresponding coefficients are 0·31 ($P = 0·23$) and

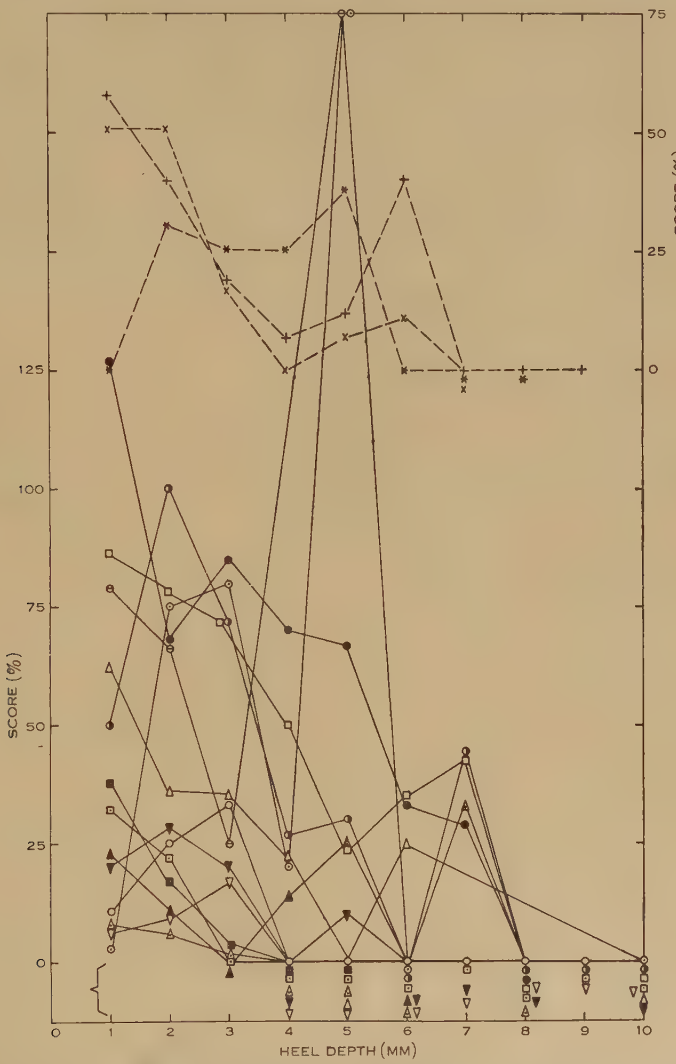

Fig. 7.—*Pinctada albina* (Lamarck). Projection of posterior ear. Score plotted against heel depth for 16 samples. For meaning of symbols see Figure 4.

0·52 ($P = 0·03$). Thus there is a slight to moderate geographical trend significant at about the 5 per cent. level.

When the samples were measured it was observed that specimens with projections of anterior borders frequently possessed pronounced posterior ears. To test for an association between the two characters a contingency table was constructed. This is given in Table 7. The expected cell frequencies were calculated assuming there was no relationship between the two variables. By pooling ++ and +++ data to remove small expected cell frequencies, χ^2 was found to be 286 with 4 degrees of freedom. This represents significance at the 0·1 per cent. level. In addition inspection shows that the signs of the differences are not distributed at random, the negatives being found only at bottom left and top right. Thus there is a positive association between projection of anterior border and posterior ear. Rank correlation coefficients between the samples as listed in Tables 4 and 6 give a measure of this association. They are 0·52 ($P = 0·006$) and 0·45 ($P = 0·017$), i.e. a moderate association significant at about the 1 per cent. level. This association is in apparent contradiction to the facts that projection of anterior border is

Table 6

PROJECTION OF POSTERIOR EAR

Samples ranked in descending order of height of the peaks of the curves in Figures 6 and 7

D.V.M. Rankings			Heel Depth Rankings		
Sample	Rank		Sample	Rank	
	All Samples	Omitting Deep Water and Harbour Samples		All Samples	Omitting Deep Water and Harbour Samples
Darwin Harbour	1		Darwin Harbour	1	
Exmouth Gulf	2	1	Roebuck Bay	2	1
Mapoon	3	2	Cadell Strait	3	2
Cadell Strait	4	3	Exmouth Gulf	4	3
Roebuck Bay	5	4	Mapoon	5	4
Torres Strait	6		Friday I.	6	5
Crocodile Group	7		Torres Strait	7	
Friday I.	8	5	Groote Eylandt	8	
Dungeness I.	9	6	Crocodile Group	9	
Groote Eylandt	10		Crab I.	10	6
Crab I.	11	7	Shark Bay	11	7
Scharapa Passage	12	8	Scharapa Passage	12	8
Watawari Reef	13	9	Dungeness I.	13	9
Thursday I. Harbour	14		Watawari Reef	14	10
Shark Bay	15	10	Moreton Banks	15	11
Moreton Banks	16	11	Thursday I. Harbour	16	

a character usually found in older specimens, while projection of posterior ear is a character reaching its maximum in 1-year old specimens. However, it must be remembered that the test for association between the two characters took no account of the size of the specimens.

(*e*) *Projection of Posteroventral Border*

It is necessary to amplify the brief mention of posteroventral border in Hynd (1955) to understand fully the character investigated here. The depth of the posterior sinus, if present, helps to determine the size of the posterior ear though it is not the sole determinant. A deep sinus may also be due to a marked convexity of the postero-ventral border in juveniles. This is illustrated in Plate 10, Figure 2 (Hynd 1955). In this case it is even further exaggerated by a clump of very prominent growth processes on the posterior border. The 0 condition is illustrated in Plate 10, Figure 1; Plate 12, Figures 2, 3; Plate 10, Figure 3; Plate 11, Figure 2 (Hynd 1955). These are all young specimens in which there is no sinus but a prominent ear. In some middle-aged to old specimens there is a subsequent projection which results from failure of the hinge-line to increase while the posteroventral border continues to grow. There may be a deep sinus but only four of 3499 specimens also showed a projection of posterior ear. The + condition is seen in Plate 11, Figure 1, and the +++ condition in Plate 11, Figure 3 (Hynd 1955). The ++ condition is seen in Plate 2, Figure 1, in the present paper. The samples have been scored and the data plotted in Figures 8 and 9.

TABLE 7

CONTINGENCY TABLE FOR PROJECTION OF ANTERIOR BORDER AND PROJECTION OF POSTERIOR EAR

		Projection of Anterior Border				Totals
		0	+	++	+++	
Projection of Posterior Ear	0	2435 2326·55 +108·45	139 222·90 −83·90	47 66·79 −19·79	5 9·76 −4·76	2626
	+	583 637·01 −54·01	109 61·03 +47·97	24 18·29 +5·71	3 2·67 +0·33	719
	++	75 121·38 −46·38	42 11·63 +30·37	16 3·48 +12·52	4 0·51 +3·49	137
	+++	7 15·06 −8·06	7 1·44 +5·56	2 0·43 +1·57	1 0·06 +0·94	17
Totals		3100	297	89	13	3499

No appreciable development of the character is seen in any sample before 4 cm D.V.M. or 2 mm heel depth. Thereafter development increases steadily with age in all samples except two, in which there is no development at any stage, and up to 70 per cent. of old specimens may have this character. The graphs do not reach any significant peaks. The curves have been listed in Table 8 in descending order of the areas lying under them. The rank correlation coefficients between these rankings and those of Table 1 are −0·20 ($P = 0·31$) and −0·28 ($P = 0·16$) when all samples are included. Omitting deep water and harbour samples the corres-

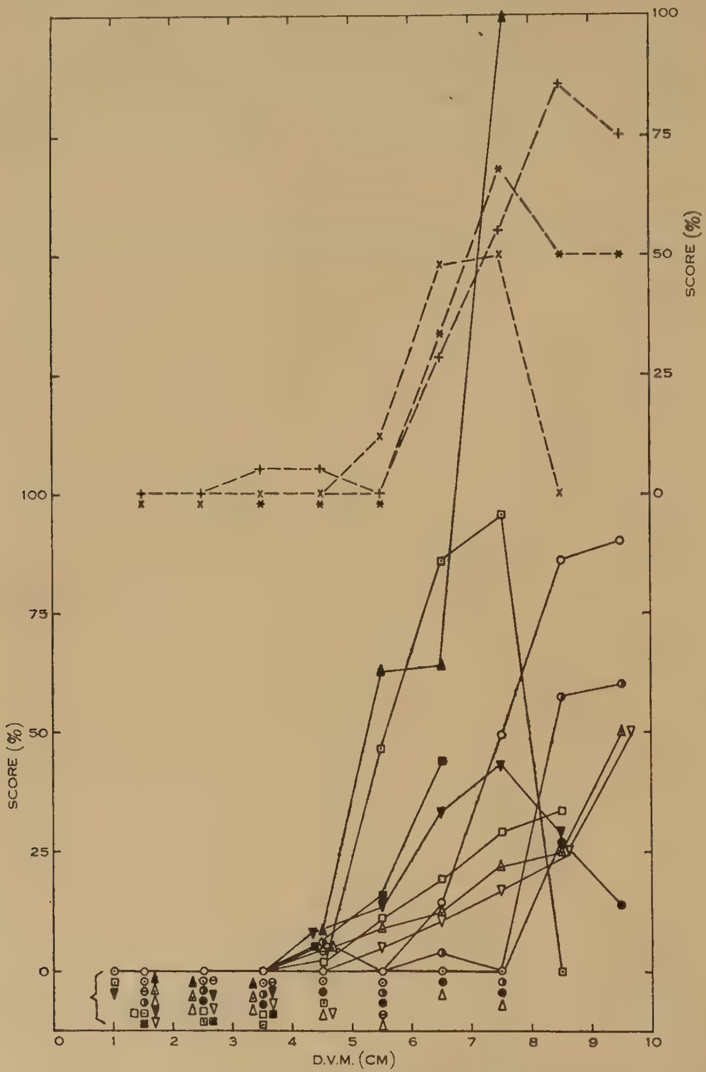

Fig. 8.—*Pinctada albina* (Lamarck). Projection of posteroventral border. Score plotted against D.V.M. for 16 samples. For meaning of symbols see Figure 4.

ponding coefficients are $-0 \cdot 19$ ($P = 0 \cdot 47$) and $-0 \cdot 13$ ($P = 0 \cdot 63$). Thus no geographic trend from west to east can be demonstrated.

It was shown above that projection of posterior ear and posteroventral border were almost mutually exclusive in individual specimens, i.e. the correlation between them is negative and almost perfect. It has also been shown that there is a moderate degree of association between projection of anterior border and posterior ear. It remains to test the association between projection of anterior border and posteroventral border.

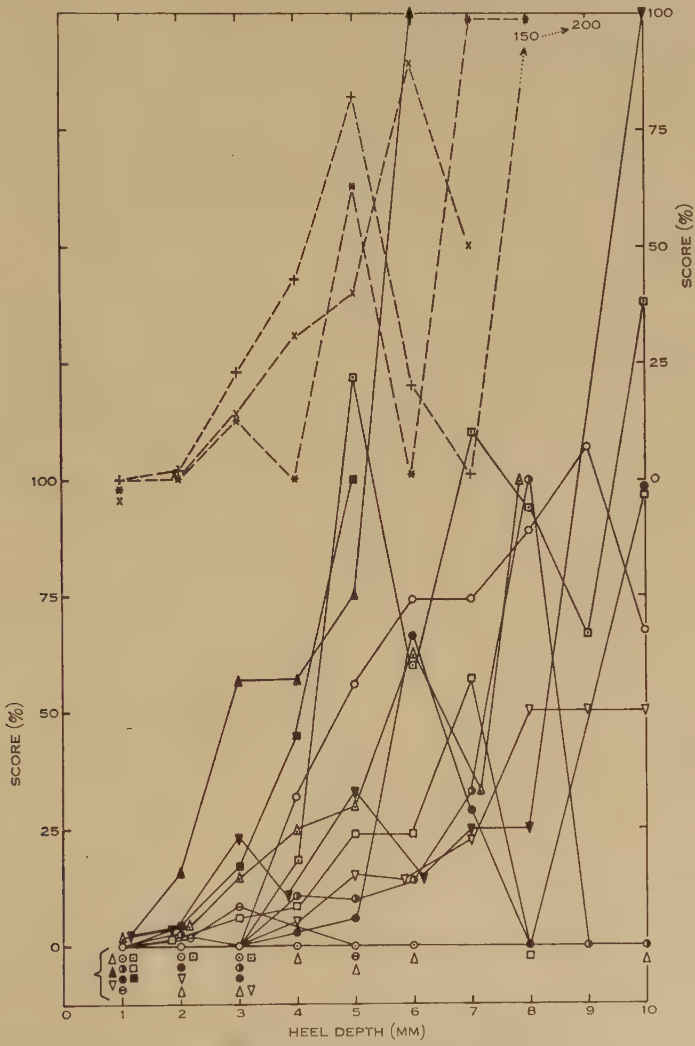

Fig. 9.—*Pinctada albina* (Lamarck). Projection of posteroventral border. Score plotted against heel depth for 16 samples. For meaning of symbols see Figure 4.

Table 9 gives the contingencies of projection of anterior border and posteroventral border for all specimens of all samples. The expected cell frequencies have been calculated assuming that development of the two characters is completely independent. After pooling ++ and +++ data to remove small expected cell frequencies, χ^2 was 26·6 with 4 degrees of freedom which represents significance at the 0·1 per cent. level. Also inspection shows that the signs of the differences are not distributed at random, but in a pattern which supports the assumption that development of the two characters is mutually exclusive in part. Rank correlation coefficients between the samples as listed in Tables 4 and 8 give a measure of this association. They are $-0\cdot49$ ($P = 0\cdot009$) and $-0\cdot57$ ($P = 0\cdot003$) i.e. a moderate negative association significant at the 1 per cent. level.

TABLE 8

PROJECTION OF POSTEROVENTRAL BORDER

Samples ranked in descending order of area beneath the curves in Figures 8 and 9

D.V.M. Rankings			Heel Depth Rankings		
Sample	Rank		Sample	Rank	
	All Samples	Omitting Deep Water and Harbour Samples		All Samples	Omitting Deep Water and Harbour Samples
Watawari Reef	1	1	Watawari Reef	1	1
Scharapa Passage	2	2	Torres Strait	2	
Crab I.	3	3	Crab I.	3	2
Groote Eylandt	4		Shark Bay	4	3
Dungeness I.	5	4	Groote Eylandt	5	
Torres Strait	6		Scharapa Passage	6	4
Crocodile Group	7		Thursday I. Harbour	7	
Cadell Strait	8	5	Dungeness I.	8	5
Shark Bay	9	6	Cadell Strait	9	6
Thursday I. Harbour	10		Moreton Banks	10	7
Moreton Banks	11	7	Crocodile Group	11	
Roebuck Bay	12	8	Roebuck Bay	12	8
Darwin Harbour	13		Mapoon	13	9
Mapoon	14	9	Darwin Harbour	14	
Friday I.	15	10	Friday I.	15	10
Exmouth Gulf	16	11	Exmouth Gulf	16	11

It has already been shown that projection of anterior border is associated with a rocky environment. There should therefore be a negative correlation between projection of posteroventral border and rocky environment. The correlation coefficients between the samples as listed in Tables 5 and 8 are $-0\cdot54$ ($P = 0\cdot03$) and

−0·62 ($P = 0·014$), i.e. a moderate negative correlation significant at the 5 per cent. level. The partial correlation coefficients of posteroventral border and rocky environment excluding geographical distribution are −0·53 and −0·61.

(*f*) *Form of Shell*

The exact connotation of this term is given by Hynd (1955). It is not the same thing as shape or outline of shell but is determined exclusively by the direction of the reference axis at the distal border. In the present study, when the angle between the tangent to the reference axis at the distal border and the hinge-line (looking posteriorly) was less than 80°, the shell was recorded as oblique; between 80° and 100° as erect; and when greater than 100° as obtuse. The specimens shown in Plate 9, Figure 3 (Hynd 1955), are both oblique. Those in Plate 10, Figures 1, 2, and Plate 12, Figures 1, 3 (loc. cit.), are all typically erect. The specimen in Plate 10, Figure 3 (loc. cit.), is obtuse.

TABLE 9

CONTINGENCY TABLE OF PROJECTION OF ANTERIOR BORDER AND PROJECTION OF POSTEROVENTRAL BORDER

		Projection of Posteroventral Border				Totals
		0	+	++	+++	
Projection of Anterior Border	0	2747 2775·74 −28·74	279 258·70 +20·30	69 61·13 +7·87	5 4·43 +0·57	3100
	+	289 265·93 +23·07	8 24·79 −16·79	0 5·86 −5·86	0 0·42 −0·42	297
	++	85 79·69 +5·31	4 7·43 −3·43	0 1·76 −1·76	0 0·13 −0·13	89
	+++	12 11·64 +0·36	1 1·08 −0·08	0 0·26 −0·26	0 0·02 −0·02	13
Totals		3133	292	69	5	3499

The data have been recorded in the form of percentage histograms in Figures 10 and 11. Inspection of these reveals immediately that oblique specimens are found almost exclusively in the first few class intervals. There are 378 oblique specimens out of a total of 3499. Of these only 40 are over 3·0 cm D.V.M. and 29 over 1 mm heel depth. All specimens of 1·0 cm D.V.M. or less are oblique. Thus obliquity is an attribute of juvenile specimens and the condition is lost with age.

Obtuse specimens number only 41 out of 3499 so the condition is comparatively rare. Of these, only one measured less than 3·0 cm D.V.M. and only four less than 2 mm heel depth. Thus obtuseness is an attribute of older specimens. It is clear that form of shell is determined principally by growth, all small specimens are oblique, most middle-sized specimens are erect, and a few middle-sized and large specimens may be obtuse.

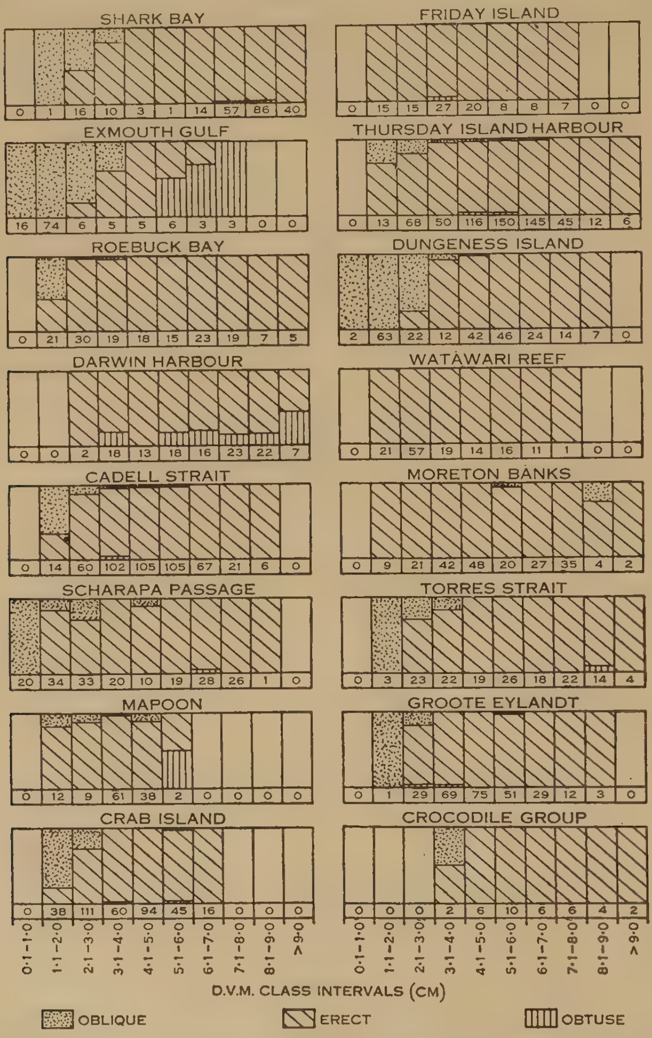

Fig. 10.—*Pinctada albina* (Lamarck). Form of shell. Histograms for 16 samples showing percentage of each form by cm class intervals of D.V.M.

There were obvious significant differences between some of the samples in the D.V.M. at which the change from oblique to erect occurred, e.g. the Exmouth Gulf and Dungeness Island samples were 100 per cent. oblique from 1·1 to 2·0 cm

D.V.M. while the Friday Island, Watawari Reef, and Moreton Banks samples were 100 per cent. erect at this size. Table 10 shows the percentage of oblique and erect specimens in the 1·1 to 2·0 cm class intervals of those samples with nine or more specimens in the class. These samples have also been ranked by descending percentages of oblique specimens (or ascending percentages of erect). The rank correlation coefficient between this ranking and the samples ranked coastwise from west to east is 0·44 ($P = 0{\cdot}10$) which is not significant.

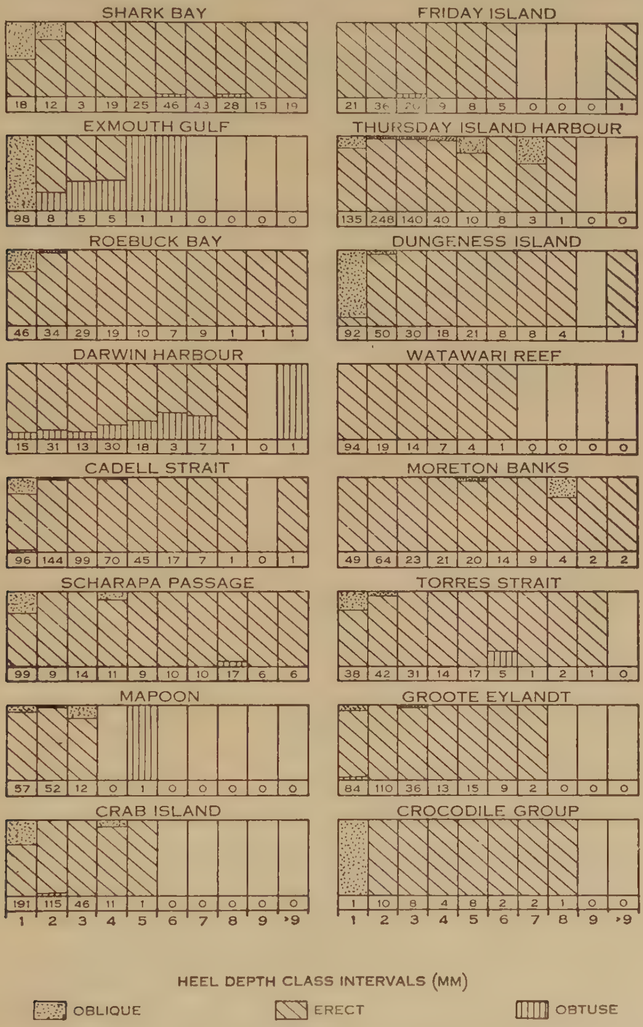

Fig. 11.—*Pinctada albina* (Lamarck). Form of shell. Histograms for 16 samples showing percentage of each form by mm class intervals of heel depth.

Inspection also reveals that the Western Australian and Darwin Harbour samples contain a greater proportion of obtuse specimens in the higher class intervals than the eastern samples. Table 11 gives the contingencies for obtuse against erect plus oblique, in the western group, Darwin Harbour, and eastern group specimens over 4·0 cm D.V.M. The expected cell frequencies have been calculated assuming there is no difference between groups. By pooling western group and Darwin Harbour data to remove small expected cell frequencies, χ^2 was found to be 64 with 1 degree of freedom, which is significant at the 0·1 per cent. level. To check that there were no significant differences within each group, tables were constructed for each group of the contingencies of obtuse against erect plus oblique in the 4·1–7·0 cm D.V.M. range and the over 7·0 cm range. χ^2 tests revealed no significant differences in any group. Therefore obtuse shells occur more frequently in the western group and Darwin Habour samples than in the eastern group.

Table 10

SAMPLES RANKED ACCORDING TO THE PERCENTAGES OF OBLIQUE AND ERECT SPECIMENS IN THE 1·1–2·0 CM D.V.M. CLASS INTERVAL*

Samples	No. of Specimens	Oblique (%)	Erect (%)	Rank
Exmouth Gulf	74	100	0	1½
Dungeness I.	63	100	0	1½
Crab I.	38	79	21	3
Cadell Strait	14	64	36	4
Roebuck Bay	21	57	43	5
Thursday I. Harbour	13	31	69	6
Mapoon	12	17	83	7
Scharapa Passage	34	15	85	8
Friday I.	15	0	100	10
Watawari Reef	21	0	100	10
Moreton Banks	9	0	100	10

* Samples with low or nil frequencies omitted.

A contingency table correlating anterior border and obtuse form of shell is given in Table 12. The expected cell frequencies were calculated assuming that the two characters were mutually independent. It can be seen at once that the differences are large and the signs are regularly distributed. By pooling erect and obtuse data and also ++ and +++ data to remove small expected cell frequencies, χ^2 was found to be 47 with 2 degrees of freedom, which is significant at the 0·1 per cent. level. By omitting oblique data and pooling +, ++, and +++ data, χ^2 was found to be 185 with 1 degree of freedom, which is also significant at the 0·1 per cent. level. Thus there is a strong positive association between the characters such that oblique specimens show little projection of anterior border (1 per cent. showed a + condition) while erect and obtuse specimens show progressively greater projection (12 per cent. and 83 per cent. respectively showed a + or better condition).

It was shown above that projection of anterior border was closely linked with projection of posterior ear and posteroventral border. Accordingly contingency tables were constructed for projection of posterior ear and form of shell and for

TABLE 11

CONTINGENCY TABLE OF FORM OF SHELL AND GEOGRAPHICAL GROUPS IN SPECIMENS OVER 4 CM D.V.M.

		Geographical Groups			Totals
		Western	Darwin Harbour	Eastern	
Form of Shell	Oblique plus erect	294 299·56 −5·56	84 97·24 −13·24	1385 1366·20 +18·80	1763
	Obtuse	11 5·44 +5·56	15 1·76 +13·24	6 24·80 −18·80	32
Totals		305	99	1391	1795

TABLE 12

CONTINGENCY TABLE OF PROJECTION OF ANTERIOR BORDER AND FORM OF SHELL

		Projection of Anterior Border				Totals
		0	+	++	+++	
Form of Shell	Oblique	375 99% 334·90 +40·10	3 1% 32·09 −29·09	0 0% 9·61 −9·61	0 0% 1·40 −1·40	378 100%
	Erect	2718 88% 2728·78 −10·78	285 9% 261·43 +23·57	73 2% 78·34 −5·34	4 0·1% 11·44 −7·44	3080 99·1%
	Obtuse	7 17% 36·32 −29·32	9 22% 3·48 +5·52	16 39% 1·04 +14·96	9 22% 0·15 +8·85	41 100%
Totals		3100	297	89	13	3499

Table 13

CONTINGENCY TABLE OF PROJECTION OF POSTERIOR EAR AND FORM OF SHELL

		Projection of Posterior Ear				Totals
		0	+	++	+++	
Form of Shell	Oblique	323 85% 283·69 +39·31	48 13% 77·67 −29·67	6 2% 14·80 −8·80	1 0·3% 1·84 −0·84	378 100·3%
	Erect	2287 74% 2311·54 −24·54	662 21% 632·90 +29·10	117 4% 120·59 −3·59	14 0·5% 14·96 −0·96	3080 99·5%
	Obtuse	16 39% 30·77 −14·77	9 22% 8·42 +0·58	14 34% 1·61 +12·39	2 5% 0·20 +1·80	41 100%
Totals		2626	719	137	17	3499

Table 14

CONTINGENCY TABLE OF PROJECTION OF POSTEROVENTRAL BORDER AND FORM OF SHELL

		Projection of Posteroventral Border				Totals
		0	+	++	+++	
Form of Shell	Oblique	368 97% 338·46 +29·54	10 3% 31·55 −21·55	0 0% 7·45 −7·45	0 0% 0·54 −0·54	378 100%
	Erect	2726 89% 2757·83 −31·83	280 9% 257·03 +22·97	69 2% 60·74 +8·26	5 0·2% 4·40 +0·60	3080 100·2%
	Obtuse	39 95% 36·71 +2·29	2 5% 3·42 −1·42	0 0% 0·81 −0·81	0 0% 0·06 −0·06	41 100%
Totals		3133	292	69	5	3499

posteroventral border and form of shell. These are given in Tables 13 and 14 respectively. The expected cell frequencies have been calculated assuming no relationship. It will be seen that with the exception of row 3 of Table 14 the differences are large and the signs regularly distributed. In Table 13, by pooling erect and obtuse data and ++ and +++ data, χ^2 was found to be 25 with 2 degrees of freedom which is significant at the 0·1 per cent. level. In Table 14 by similar pooling χ^2 was found to be 28 with 2 degrees of freedom which is also significant at the 0·1 per cent. level. However in this table when the oblique data were omitted and ++ and +++ data pooled, χ^2 was found to be 1·985 with 2 degrees of freedom which corresponds to a probability of about 0·4, i.e. the differences are not significant.

TABLE 15

ASSOCIATIONS BETWEEN PROJECTION OF ANTERIOR BORDER, PROJECTION OF POSTERIOR EAR, PROJECTION OF POSTEROVENTRAL BORDER, AND FORM OF SHELL

	Projection of Posterior Ear	Projection of Posteroventral Border	Form of Shell
Projection of anterior border	Moderate positive association	Moderate negative association	Strong positive association
Projection of posterior ear		Almost mutually exclusive	Moderate positive association
Projection of posteroventral border			Oblique form has moderate negative association. Erect and obtuse forms are mutually independent

There is a moderate positive association between projection of posterior ear and form of shell such that the proportion of shells with projection of posterior ear is much higher in the obtuse category. Only 15 per cent. of oblique and 26 per cent. of erect shells show any development compared with 61 per cent. of obtuse shells. There is a moderate negative association between projection of posteroventral border and form of shell in that oblique specimens contain a significantly smaller proportion of shells with any projection than the erect and obtuse specimens. This fact was to be expected, as nearly all oblique shells are young and projection of posteroventral border is associated with older specimens. In older specimens form of shell and projection of posteroventral border are mutually independent. All the foregoing associations can be clearly seen in Table 15.

(*g*) *Colour Pattern*

The percentage histograms for each sample are given in Figures 12 and 13. Inspection reveals that the samples fall into the same groups as in D.V.M.–heel depth relationship. There is a western intertidal group with a large proportion of light shells and a small proportion of rayed. There is an eastern intertidal group with a small proportion of light shells, and a large proportion of rayed. The Darwin Harbour sample is again intermediate. In addition there is a group of eastern deep water samples showing a moderately large proportion of light shells and a moderately small proportion of rayed. χ^2 tests showed that these groups all differ significantly (at the 0·1 per cent. level) from one another except that there is no significant difference between Darwin Harbour and the deep water group.

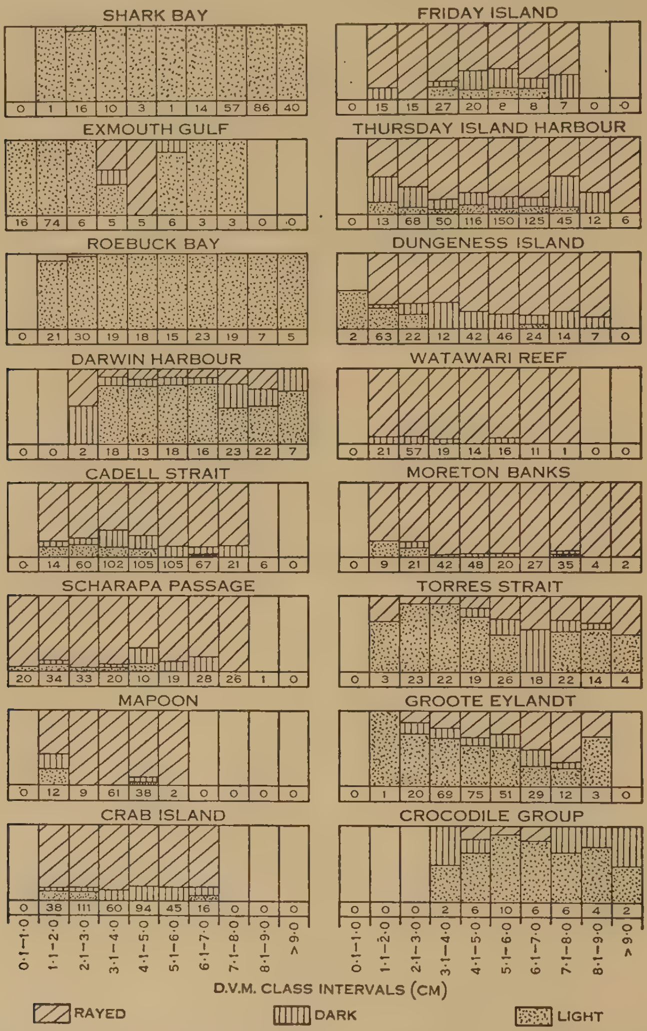

Fig. 12.—*Pinctada albina* (Lamarck). Colour pattern. Histograms for 16 samples showing percentage of each pattern by cm class intervals of D.V.M.

The data for intertidal samples are summarized graphically in Figure 14 where the percentage of light shells is plotted against the easterly distance of each sample from Shark Bay. It is immediately obvious that the eastern and western groups are separated by a prominent cline, the Darwin Harbour sample being situated approximately in the centre. It is highly probable that there is a cline to the southward of Shark Bay also as the three specimens from Leighton were all prominently rayed.

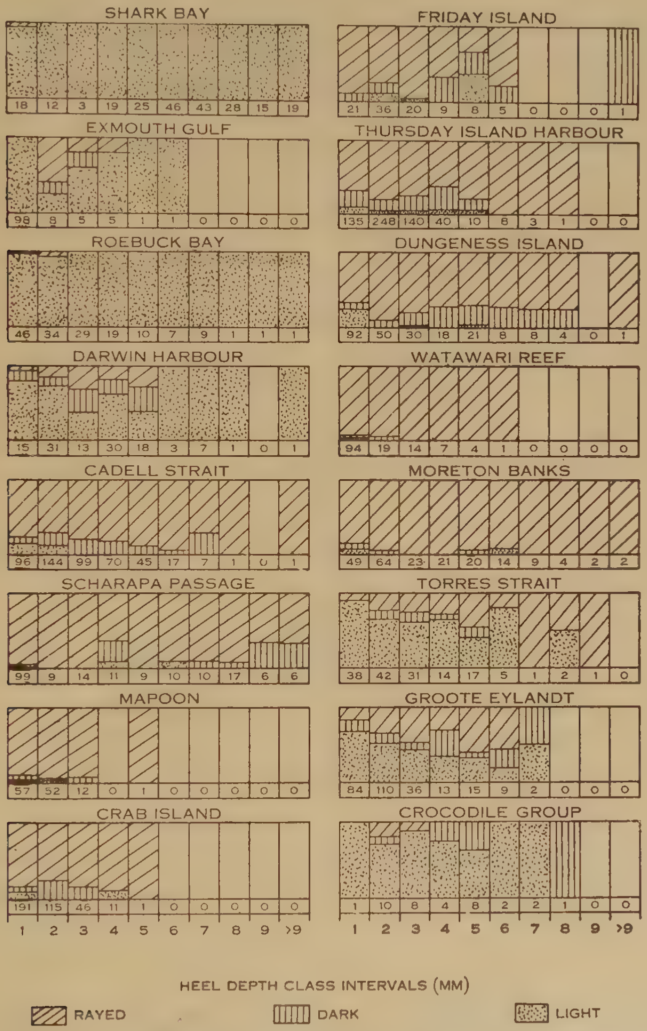

Fig. 13.—*Pinctada albina* (Lamarck). Colour pattern. Histograms for 16 samples showing percentage of each pattern by mm class intervals of heel depth.

Some of the variations observed within groups of samples are statistically significant, e.g. the Exmouth Gulf sample differs from the remainder of the western intertidal group in having seven rayed and two dark specimens out of 118, while there are only four rayed specimens out of 385 in the remainder of the group. There is also a significantly higher proportion of dark specimens in the Thursday Island Harbour sample as compared with the remainder of the eastern intertidal group.

It is also possible to demonstrate trends within samples in the eastern intertidal group. A contingency table was constructed for the Crab Island sample showing numbers of each type of colour pattern in each class interval of D.V.M. The expected cell frequencies were calculated assuming that the proportion of each colour pattern was independent of D.V.M. χ^2 was found to be 29 with 10 degrees of freedom which is significant at the 1 per cent. level. Accordingly the mean D.V.M. for each colour pattern of each sample was calculated and it was found that the light specimens had a lower measurement than the dark or rayed specimens in every sample.

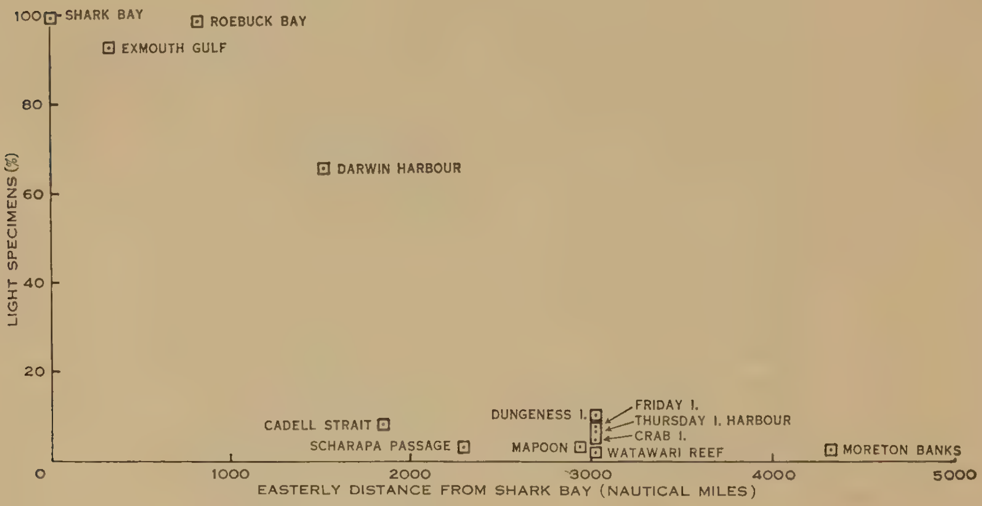

Fig. 14.—*Pinctada albina* (Lamarck). Colour pattern. Percentage of light specimens in intertidal samples plotted against easterly distance from Shark Bay.

A *t* test confirmed the significance of this difference ($t = 3 \cdot 694$ on 8 degrees of freedom, $P < 0 \cdot 01$). There were no significant differences between the means of dark and rayed specimens. The trend is therefore towards increased pigmentation with age.

While not as light-coloured as the western intertidal group, the eastern deep water group is nevertheless much lighter in colour than its intertidal counterpart. An explanation of this has been suggested by Hynd (1955). It is apparently associated with an absence of light. Unfortunately a deep water sample from Western Australia could not be obtained. It is almost certain that it would have been predominantly light in colour, and at least as light as the intertidal samples.

It is evident then that colour pattern in the intertidal samples is largely a function of geographic position but within the eastern group, at least, depth of water and age are also important.

(*h*) *Black Band Distal to Nacre*

The nature of this character is described by Hynd (1955). Specimens in which the band extended almost completely from anterior to posterior ear were rated as +++. Those in which there was no black band were rated 0. When the band extended over one third and two thirds of the border the specimens were rated + and ++ respectively. The ++ condition is illustrated in Plate 10, Figure 3 (Hynd 1955), and the 0 condition in Plate 12, Figures 2, 3. The + and +++ conditions are illustrated in the present paper in Plate 2, Figure 1, and Plate 2, Figure 2, respectively.

Table 16

BLACK BAND DISTAL TO NACRE

Mean scores for samples *in toto* and dissected into two parts lying above and below 5 cm D.V.M. and 1 mm heel depth

Sample	Mean Score For Whole Sample (%)	Mean Score for Sample Dissected by D.V.M. (%)		Mean Score for Sample Dissected by Heel Depth (%)	
		0–5·0 cm	>5·0 cm	1 mm	>1 mm
Shark Bay	0	0	0	0	0
Exmouth Gulf	5	4	17	0	30
Roebuck Bay	52	57	45	39	57
Darwin Harbour	85	67	92	87	85
Cadell Strait	157	162	150	156	157
Scharapa Passage	162	170	150	164	161
Mapoon	150	150	*	146	153
Crab I.	120	123	102	127	112
Friday I.	106	105	109	143	96
Thursday I. Harbour	105	109	101	99	106
Dungeness I.	148	128	178	111	172
Watawari Reef	142	142	139	141	142
Moreton Banks	71	76	65	92	65
Torres Strait	46	24	63	18	55
Groote Eylandt	51	47	55	48	53
Crocodile Group	17	38	11	0	17

* Only two specimens had D.V.M. >5·0 cm.

The samples were scored as for other characters but in no sample were significant differences between class intervals found. Accordingly the data were not presented as a graph but in reduced tabular form (Table 16). Comparisons between columns 3 and 4, and 5 and 6 of this table reveal that the differences between young and old specimens are small.

Inspection of the second column of the table shows that the samples are divided into exactly the same groups as for colour pattern. There is a western intertidal group with low scores, an eastern intertidal group with high scores, and an eastern deep water group with moderately low scores. The Darwin Harbour sample is again intermediate between the western intertidal and the eastern intertidal groups.

The mean score of each of the intertidal samples is plotted in Figure 15 against the easterly distance from Shark Bay. This reveals that the eastern and western groups are separated by a cline. At the same time there are differences within the groups. The Moreton Banks sample is conspicuously lower in score than the rest of the eastern group, and a *t* test showed that this difference was significant ($t = 2 \cdot 71$ on 7 degrees of freedom, $0 \cdot 02 < P < 0 \cdot 05$). It is possible then that there is a cline at the eastern end of the range also. The Roebuck Bay sample is higher in score than the rest of the western group, but a *t* test showed this to be of doubtful significance ($t = 10 \cdot 4$ on 1 degree of freedom, $0 \cdot 05 < P < 0 \cdot 10$). The three specimens from Leighton were rated + or ++ for black band so there may be a third cline at the western end of the range.

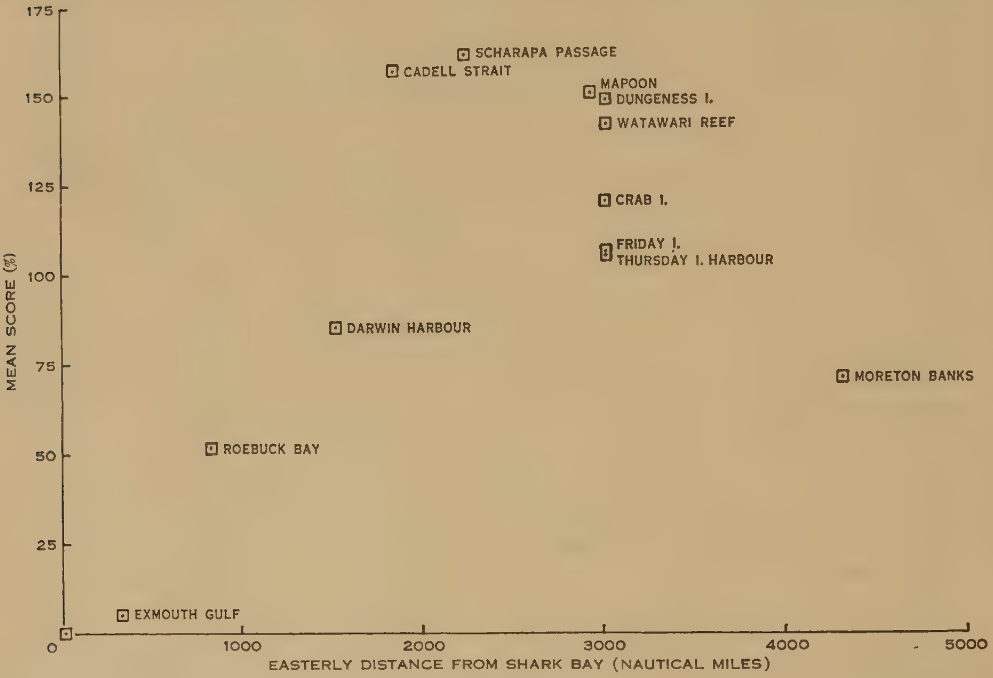

Fig. 15.—*Pinctada albina* (Lamarck). Black band distal to nacre. Mean score for intertidal samples plotted against easterly distance from Shark Bay.

The moderately low scores of the eastern deep water group as compared to the eastern intertidal group show that development of black band decreases with depth in the same manner as colour pattern.

These similarities between black band and colour pattern suggest that there may be an association between them. In fact it was observed when the specimens were being measured that light specimens rarely possessed a black band while rayed or dark specimens usually possessed a moderately or strongly developed black band.

Accordingly a contingency table was prepared and is given in Table 17. The expected frequencies were calculated assuming no relationship between the characters. It is immediately obvious that the differences are large and the signs regularly distributed. By pooling ++ and +++ data, χ^2 was found to be 1000 with 4 degrees of freedom which is significant at the 0·1 per cent. level. Development of a black band is therefore strongly associated with rayed or dark specimens, and lack of a black band with light specimens.

TABLE 17

CONTINGENCY TABLE OF COLOUR PATTERN AND BLACK BAND DISTAL TO NACRE

		Black Band				Totals
		0	+	++	+++	
Colour Pattern	Light	759 361·35 +397·65	173 315·05 −142·05	62 276·41 −214·41	0 41·19 −41·19	994
	Rayed	443 776·87 −333·87	820 677·32 +142·68	764 594·26 +169·74	110 88·56 +21·44	2137
	Dark	70 133·78 −63·78	116 116·64 −0·64	147 102·33 +44·67	35 15·25 +19·75	368
Totals		1272	1109	973	145	3499

(*i*) *Yellow Nacre*

"Yellow nacre" appears as a variety of colours ranging from greenish yellow to orange. Even occasional pinkish specimens are seen. The colour of the lip of an average specimen of gold-lipped *P. maxima* from Torres Strait was taken as the +++ standard. The other standards were intermediate between this and the normal silvery colour which was the 0 condition. In practice no difficulty was caused by the variety of colours presented.

The data are presented in Figures 16 and 17. Inspection of these graphs shows that yellow nacre is a characteristic of older specimens. It was almost completely absent in specimens of a few cm D.V.M. or 1 mm heel depth. Thereafter in most samples both the proportion of specimens with yellow nacre and the intensity of the yellow increased. In some samples as many as 70 per cent. of the older specimens showed some development of the colour; in other samples, it was almost completely absent.

The samples are listed in Table 18 in descending order of area beneath the curves in Figures 16 and 17. The correlation coefficients between the samples so ranked and ranked geographically, are zero ($P = 1·00$) and 0·03 ($P = 0·95$) which shows that there is no geographical trend in the character.

The differences between samples do not seem to be associated with any known ecological condition. No such condition suggested itself for investigation when the samples were being collected, nor does there appear to be any association with rocky environment, as inspection of the Torres Strait group of samples shows. Of these five samples, the Crab Island, Friday Island, and Thursday Island Harbour samples have low scores while the Dungeness Island and Watawari Reef samples have high scores. Crab Island and Watawari Reef are grassy bank environments, and Friday Island and Dungeness Island are rocky.

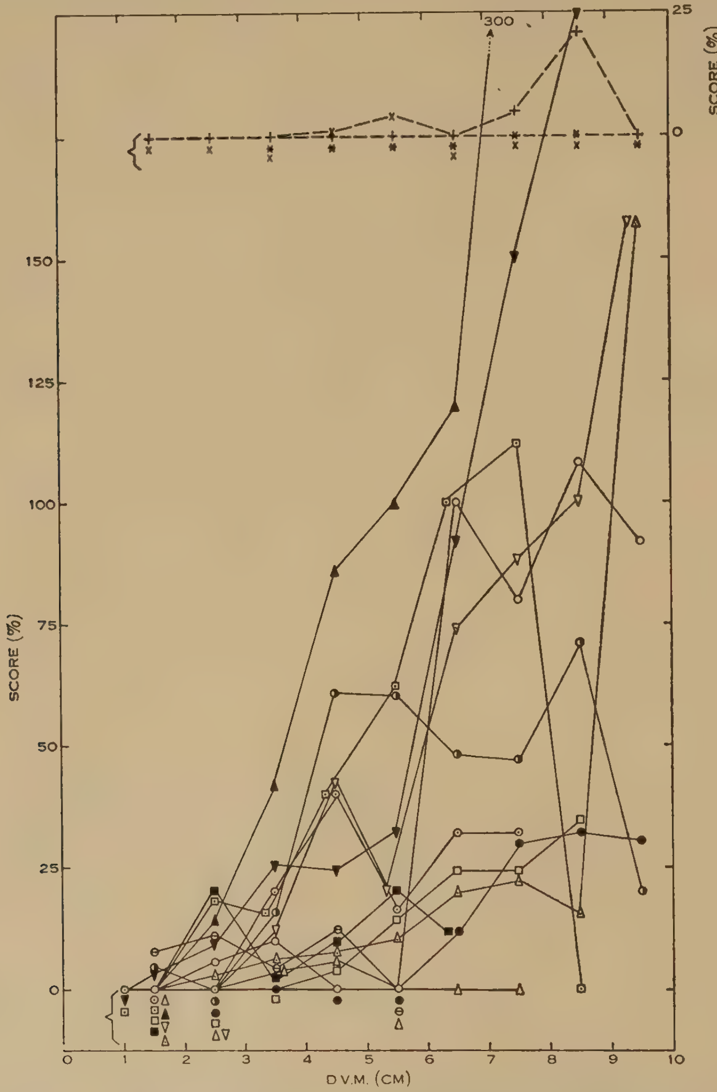

Fig. 16.—*Pinctada albina* (Lamarck). Yellow nacre. Score plotted against D.V.M. for 16 samples. For meaning of symbols see Figure 4.

The deep water samples show very little development of yellow colour. In view of the wide variation in the intertidal samples, however, and the fact that there are only three deep water samples, it cannot be assumed that this is the normal condition for deep water specimens.

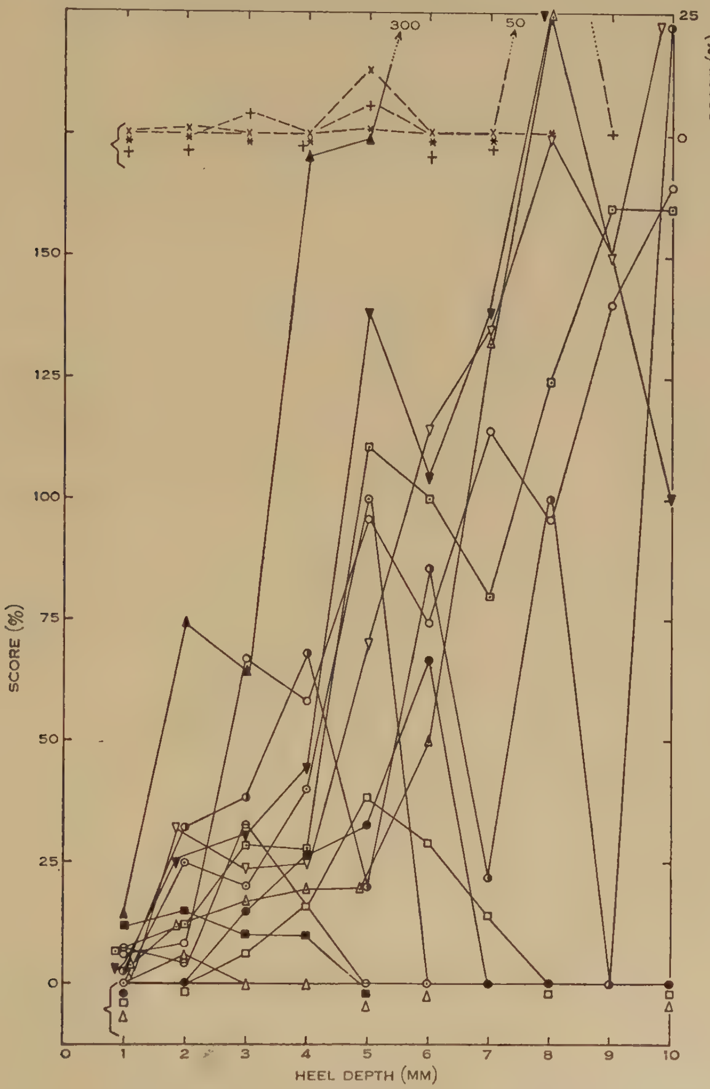

Fig. 17.—*Pinctada albina* (Lamarck). Yellow nacre. Score plotted against heel depth for 16 samples. For meaning of symbols see Figure 4.

IV. Discussion

Most of the characters investigated fall into one of two well-defined and unrelated categories. The first contains those characters associated with shape of the shell, i.e. projection of anterior border, posterior ear, posteroventral border, and form of shell. It has been shown that they are closely interrelated, that none of them shows a geographical trend (except slight trends in projection of posterior ear and posteroventral border), but that they all differ depending on environmental conditions. The second contains characters associated with the colour of the shell, i.e. colour pattern and black band distal to nacre. These are closely interrelated, with no ecological association, but they do show a geographical trend.

Investigation of the first category has shown that because of the relationship between the various characters, deviations from the normal shape of shell follow two well-defined lines. In the first, the anterior border and posterior ear project strongly, the posteroventral border does not project, and the shell form is obtuse. In the second, the anterior border and posterior ear do not project, the posteroventral border projects strongly, and the shell form is oblique or erect. These two extremes are of course very distinctive and the former has been given the specific name *fimbriata* (Reeve 1857). These forms are the result of environmental influence and do not constitute separate species or even subspecies.

TABLE 18

YELLOW NACRE

Samples* ranked in descending order of area beneath the curves in Figures 16 and 17

D.V.M. Rankings		Heel Depth Rankings	
Sample	Rank	Sample	Rank
Watawari Reef	1	Watawari Reef	1
Scharapa Passage	2	Dungeness I.	2
Dungeness I.	3	Moreton Banks	3
Shark Bay	4	Scharapa Passage	4
Moreton Banks	5	Shark Bay	5
Roebuck Bay	6	Roebuck Bay	6
Exmouth Gulf	7	Exmouth Gulf	7
Crab I.	8	Mapoon	8
Mapoon	9	Darwin Harbour	9
Cadell Strait	10	Thursday I. Harbour	10
Thursday I. Harbour	11	Cadell Strait	11
Darwin Harbour	12	Crab I.	12
Friday I.	13	Friday I.	13

* Deep water samples omitted.

Investigation of the second category has demonstrated the probability of clines separating the species into western and eastern populations. D.V.M.–heel depth relationship shows a discontinuity in exactly the same part of the range, enhancing the value of the evidence of the other two characters. Following Huxley (1939, 1940), these populations are regarded as subspecies. Since these subspecies are defined by statistical criteria it is impossible to identify single specimens on morphological grounds alone. Locality then becomes the sole criterion. This is important because it influences the names to be applied to the subspecies.

P. albina was described by Lamarck (1819) from Tasmania. However, this type locality is incorrect as the range of the species does not extend so far. The lectotype selected by Hynd (1955) bears the label "Oceanie" which was shown to correspond to the Indo-Pacific area. Iredale (1939, p. 336) suggested that "Lamarck's *M. albina* is probably founded on a Shark's Bay shell" presumably only because of the similarity in colouring. It is thus impossible to determine whether or not the lectotype came from northern Western Australia. However, Shark Bay is now selected as "designated typical locality" under Article 17, Section *a*,2 of the Draft Rules of the International Code of Zoological Nomenclature (Bradley 1957). Thus the western subspecies assumes the name *P. albina albina*, and *carchariarum* Jameson becomes a synonym.

In Hynd (1955), *sugillata* Reeve was selected as the name for the eastern subspecies, pending examination of the types of *atropurpurea* Dunker and *rutila* Reeve. No type locality was given by Dunker (1852) for *atropurpurea* and the holotype is not in the Zoological Museum, Amsterdam, or the Löbbecke Museum, Düsseldorf, both of which acquired parts of the Scheepmaker shell collection which originally contained Dunker's holotype (van Benthem Jutting 1939 and personal communication). It is almost certain that the holotype has been lost and therefore synonymy or otherwise with *albina* Lamarck cannot be proved. The original description and figure are inadequate. Thus the name is not available for the eastern subspecies. Reeve (1857) gave Australia as the type locality of *rutila* and also stated that the collector was Strange. Iredale (1939) stated that Strange collected at Sydney. Sydney is therefore regarded as the type locality for *rutila* Reeve. Dr. S. P. Dance of the British Museum (Natural History) has examined the holotype of *rutila* Reeve and pronounces it (personal communication) to be conspecific with *perrutila* Iredale, regarded by Hynd (1955) as a synonym of *sugillata* Reeve. Therefore *rutila* Reeve is available for the eastern subspecies. As the present investigation did not include any sample from Sydney, it would be unwise to assume that the eastern subspecies extends unchanged to Sydney. Thus *rutila* Reeve cannot yet be applied, and *sugillata* Reeve is retained for the eastern subspecies.

V. Acknowledgments

The author is indebted to the following persons for the donation of specimens or assistance in making collections: B. C. Cotton, A. J. Fraser, N. Le Grand, H. N. Shepherdson, J. L. H. Wassell, Captain F. Wells, V. Wells. Help in tracing type specimens was received from Drs. van Benthem Jutting of the Zoological Museum, Amsterdam, and W. J. Rees, I. C. J. Galbraith, and S. P. Dance of the British Museum (Natural History).

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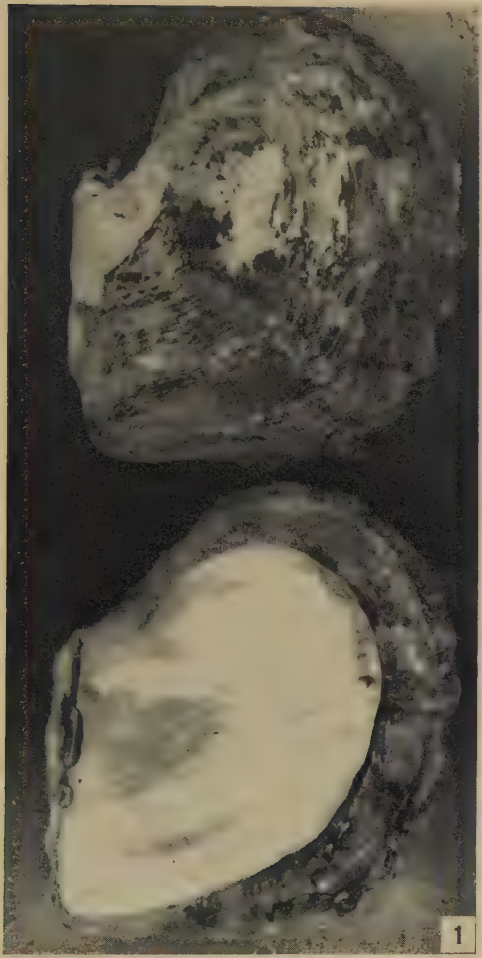

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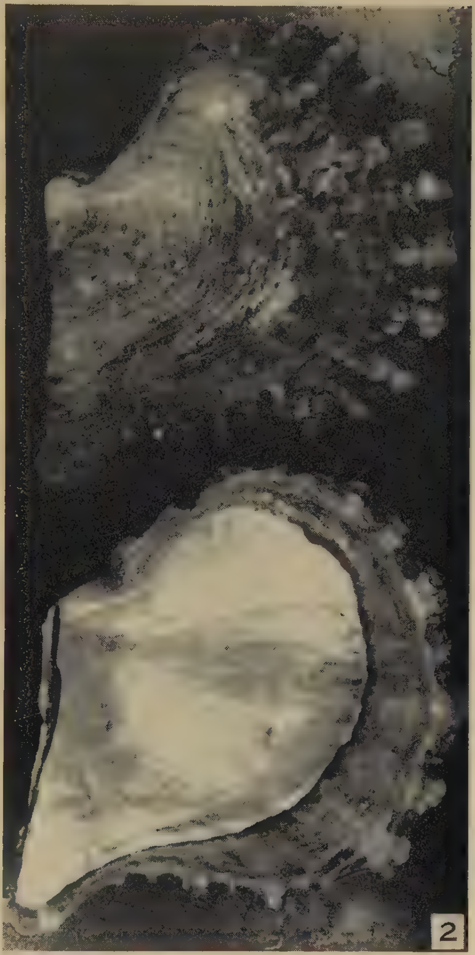

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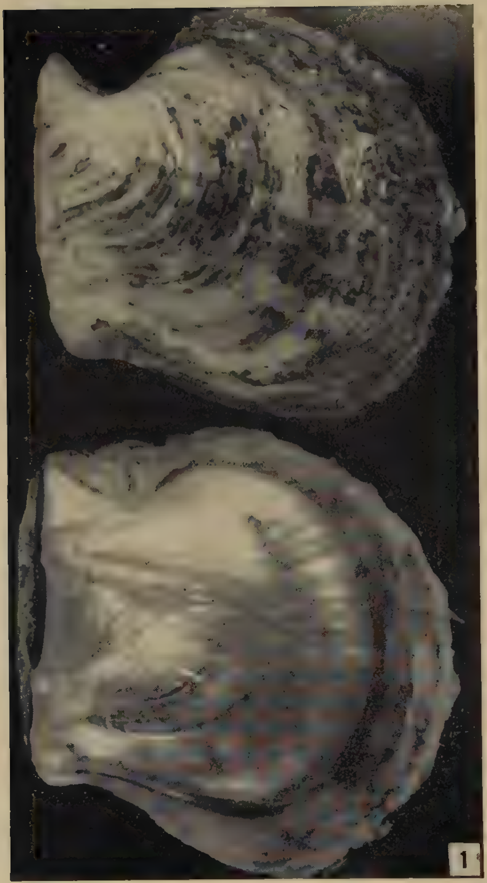
Fig. 1.—*P. albina sugillata* (Reeve) from intertidal zone, Little Lagoon, Groote Eylandt, 23.vii.1952, showing + + + projection of the anterior border. Note also the deformed ligament.
Fig. 2.—*P. albina albina–sugillata* cline specimen from wharf piles, Darwin Harbour, 10.x.1956, showing + + + projection of the posterior ear and slightly more than + + development of the black band distal to the nacre.

ANALYSIS OF VARIATION IN PINCTADA ALBINA



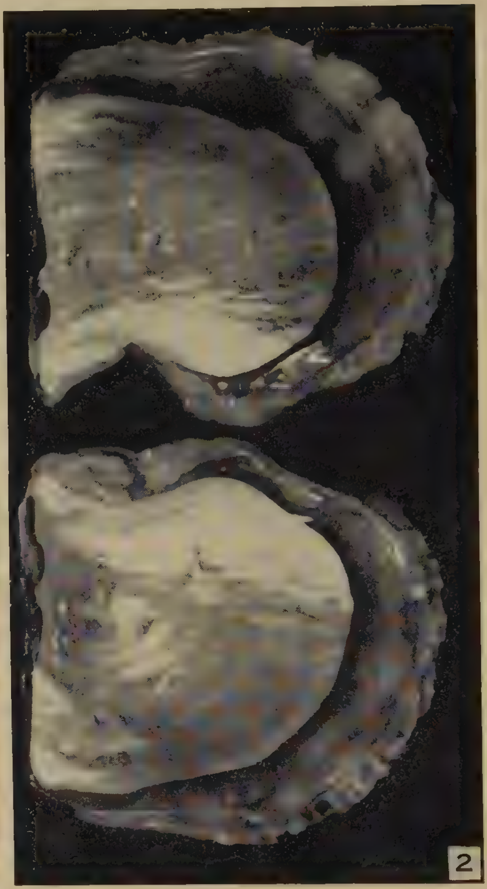


Fig. 1.—*P. albina sugillata* (Reeve) from intertidal zone, Iwaitcha Bay, Groote Eylandt, 22.viii.1952, showing ++ projection of the posteroventral border.

Fig. 2.—*P. albina sugillata* (Reeve) from intertidal zone, Little Lagoon, Groote Eylandt, 23.vii.1952, showing +++ development of the black band distal to the nacre. Note also the deformed ligament.

THE DEVELOPMENT OF THE EMBRYO AND MEMBRANES OF THE HUMPBACK WHALE, *MEGAPTERA NODOSA* (BONNATERRE)

By C. W. Stump,* J. P. Robins,† and Mary L. Garde*

[*Manuscript received May* 3, 1960]

Summary

The material consists of 20 embryos (5--30 mm) and two foetuses (63 mm and 90 mm) collected at whaling stations on Moreton and Norfolk Islands (latitude 27° 11′ S. and 29° 5′ S. respectively) during late August, September, and early October in 1952–53–54 and 1956. The consecutive series permitted the study of membrane formation and organogenesis.

Younger embryos are found in grooves between the folds of endometrium in a constant site in that uterine horn associated with the ovary containing the recent corpus luteum.

Older embryos and the early foetus are adapted to lie freely in the uterine fluid, and are devoid of any mechanism for apposition or attachment to the endometrium.

Variation in the sequence of the association of the components of the umbilical cord provides suspensory structures for the amnion and yolk sac, and for the embryo a bifid ligament, retained in the early foetus for attachment of the foetal membranes.

In the younger foetus the allantoic duct drains the nephric secretion into the uterine cavity. In the older foetus chorionic villi are present. The bifid suspensory ligament forms the major part of the distal region of the umbilical cord. The allantoic duct is reunited with the allantoic sac.

Amniogenesis is by folding. During the embryonic period the chorio-amniotic connection forms a suspensory ligament. The yolk sac, attached by a novel ligament to the amnion, is large and functional in the embryo. In the foetus vascular splanchnopleure is present in a tubular form.

A rete system develops in the embryo.

I. Introduction

The seasonal distribution of humpback whales in the southern hemisphere indicates that most are found in the Antarctic during the summer, and that during the winter a migration to tropical seas occurs. The migration north is related to mating and breeding, although the sexually immature are included. Return to Antarctica at the beginning of the summer is associated with feeding.

In eastern and western Australian waters some whales begin to ovulate in late June, the majority ovulate at the end of July and in August, and some as late as November (Robins 1960). Mating is at a maximum in August. On the east Australian coast this is confirmed by the youngest embryo collected on August 18, 1954, at Tangalooma Whaling Station, Moreton I.; young embryos continued to appear to the end of the month. Older embryos and foetuses were collected from whales, which had probably commenced the migration south. It is recorded in the International Whaling Statistics that foetuses measuring 60–120 cm have been recovered in Antarctica during the summer. In the winter foetuses averaging 417 cm in length have been found on the Australian coast (Chittleborough 1958). These observations support the concept of a 12-months breeding cycle with a gestation period of 11 months.

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II. Materials and Methods

The material collected on whaling stations by one of the authors (J. P. R.) at Tangalooma, Moreton Island, and by D. J. Dunstan at Norfolk Island, comprises a series of 20 embryos in their membranes, from somite stages to the 30 mm stage, and two foetuses of 63 mm and 90 mm. The Tangalooma collection of embryos between 5·5 mm and 17 mm was made in late August and early September in 1952–53–54. Later stages (with the exception of one 6-mm embryo) came from Norfolk Island; this material was collected in late September and early October 1956, and comprised three embryos between 23 mm and 30 mm and two foetuses.

Finding of embryos was not difficult if the uterus had not filled with fluid; when a recent corpus luteum was noted in an ovary, the uterine horn of the same side was examined. In most cases an area over the middle of the antimesometrial border showed slight hyperaemia. A longitudinal incision was made above the border and continued along the length of the cornu; endometrial folds were then reflected. The embryo was found with the elongated chorionic sac lying in a groove between the folds at the site of hyperaemia. If the uterus contained fluid, a 3-in. incision only was made as above and the uterine contents passed into a fine wire gauze strainer. Embryos were recovered complete with membranes and transferred to 10 per cent. formalin.

Whales harpooned in subtropical waters undergo rapid post-mortem changes; the measure of deterioration is the time lag between killing and flensing. On the whole the material is suitable for morphological study, but some specimens had undergone extensive post-mortem changes and others evinced trauma such as rupture of the allantoic sac, coelomic haemorrhage, and tangling of the chorionic processes.

After examination of the first embryo collected in 1952 (E282, 15 mm) it was apparent that study of a consecutive series would be necessary to interpret the unusual embryo–membrane relationships.

Seventeen embryos were sectioned serially, of which nine were complete in membranes. The conventional crown–rump measurement is not applicable, but it was found that the maximum length is a practical index of state of development and it has been used throughout. For descriptive purposes the embryos are grouped according to degree of development and overall length. One millimetre separates each group from I to V; these groups cover the early stages in organogenesis and membrane differentiation, completed at 10 mm in Group V. Group VI, from 10 mm to 20 mm, illustrates growth, differentiation, and the onset of cetacean morphology; Group VII is the end of the embryonic phase. In the foetuses study is restricted to gross external features and microscopic sections of the umbilical cord and membranes.

There exists considerable literature on Cetacea, none of which is relevant to the present morphological study. On placentation the classic contributions of Turner have been extended by Wislocki and others: with this work we are familiar. We are indebted to the many anatomists who over the years have recorded the morphology of this order.

III. DESCRIPTION OF EMBRYOS AND MEMBRANES

Group I (5–5·9 mm).—The two embryos of Group I, E346 (Plate 1, Fig. 1) and E306 (Plate 1, Fig. 2), though differing developmentally both measure 5·5 mm; E346 is the younger. Respective lengths of the chorionic vesicle are 120 mm and 135 mm: difference in length of the chorionic vesicle within a group is a matter of individual variation, not a measure of its development; the same applies to the terminal form of a vesicle, which varies from a filament to a bulbous dilatation. An elongated yolk sac lies ventrally within the vesicle (Plate 1, Fig. 2); the apposed wall of the yolk sac is fused with the chorion, forming an avascular trilaminar omphalopleure. Dorsal to, and coextensive with the yolk sac, the extraembryonic coelom is bounded ventrally by the vascular splanchnopleure; the vitelline vessels are longitudinally disposed in the splanchnopleure, the site of intravascular haemopoiesis in Groups I and II. Vascular splanchnopleure and trilaminar omphalopleure are in close apposition; between these two walls the cavity of the yolk sac is reduced to a cleft. Inversion of the splanchnopleure is persistent in the series. Endoderm of the splanchnopleure is cubical, while that of the omphalopleure is flattened epithelium; staining reaction is markedly orthochromatic (Plate 12, Fig. 2). Post mortem the splanchnopleuric epithelium is shed in sheets: in the embryos of Group I only occasional plaques are to be found *in situ*, the free cells lying in the vitelline cavity. Trophoblast detaches with equal rapidity and is found only occasionally in the better-preserved specimens (Plate 12, Fig. 1) (in foetal stages it is more adherent).

E346 is in the middle somite stage (Plate 4, Fig. 1). Although the neural groove has closed, the pharyngeal arches have not yet appeared, and the buccopharyngeal membrane is intact (Plate 7, Fig. 1). In apposition to a V-shaped extremity of the flexed caudal region is a bilobed allantoic outgrowth (Plate 4, Fig. 1). The septum transversum is represented by an intracoelomic portion partitioning the cardiac from the abdominal coelom ventrally, and an extracoelomic portion, ventral to the cardiac area which attaches the amnion at its free margins (Plate 7, Fig. 1). Splanchnopleure is adherent to the caudal coelomic surface of the septum, to the ventral surface of the extraembryonic part of the septum transversum, and to the attached amnion over an area extending from the embryonic rims laterally to the head region cephalic to the stomatodaeum (Plate 4, Fig. 1, and Plate 7, Fig. 1). The fused area indicates an earlier restriction in the extent of the extraembryonic coelom cephalic to the protocardiac area. The lateral attachment of the amnion passes from the extraembryonic portion of the septum to the embryonic rim which is conjoined with the septum; haemopoietic cords, precursors of the umbilical veins, constitute the rim (Plate 7, Figs. 1 and 2). Caudally the rim is fused with the lateral allantoic lobes (Plate 4, Fig. 1).

The amnion is a fluid-free close-fitting sac, joined to the chorion by a persistent chorio-amniotic connection, in the form of a patent membranous tube of somatopleure (Plate 7, Figs. 1 and 5); later this tube is converted into a fibrous cord. It is a constant structure of the embryo of *Megaptera nodosa:* the term chorio-amniotic ligament is used in future reference.

The bilobed allantois is reminiscent of that of the pig and sheep; in the ungulates however the corresponding stage of development occurs in early somite embryos before the closure of the neural groove. An endodermal duct connects the primitive gut with the allantois in the median plane (Plate 7, Fig. 2) and forms a bicornuate tube extending into the lobes. The allantoic duct, when later associated with the umbilical arteries, constitutes the splanchnic part of the allantoic stalk. The term body stalk is inapplicable. Laterally the lobes in their caudal two-thirds fuse with the embryonic rims; the cephalic third of each lobe is expanded and free (Plate 4, Fig. 1). The haemopoietic cords of the rim terminate in the allantoic tissue; the fusion of the allantois with the embryonic rim constitutes the somatic part of the allantoic stalk. Histologically the allantois is a reticulum of avascular mesoderm with scattered foci of extravascular haemopoiesis (Plate 7, Fig. 2).

E306 is a somite embryo sectioned dorsoventrally in the coronal plane, an orientation preferred in the present study (exceptions being the previous specimen E346 and E267 of Group IV). The cranial half of the embryo is flexed at an angle of approximately 90°, involving liver, cardio-pharyngeal, and head regions. The first three pharyngeal arches are apparent (Plate 4, Fig. 2). An epithelial gut tube extends from the presumptive gastro-duodenal region into the cavity of the yolk sac, ending in a bulbous enlargement (Plate 7, Figs. 3 and 4, Plate 8, Fig. 1). Caudal to the liver the body walls are tenuous, shallow, and splayed laterally (Plate 2, Fig. 4); they contain the umbilical veins, the walls of which attach the amnion. The abdominal coelom lacks definition, apart from the grooves between the dorsal mesentery and the mesonephroi. The liver consists of a ventral mass developing in the abdominal lamina of the septum transversum, and of dorsal lobes on either side of the gut tube and of the dorsal mesogaster (Plate 7, Fig. 3). In the expanded liver region the body walls are deepened dorsoventrally, surmounted by everted lateral folds attaching the amnion; the umbilical veins lie in the junction of fold and wall (Plate 7, Fig. 3). Projecting between the body walls the liver attaches the yolk sac by a broad ventral mesentery of septal tissue. The vitelline veins enter the dorsal liver lobes from the mesentery (Plate 7, Fig. 3). The extraembryonic extension of the septum transversum is continuous with the cardiac lamina of the septum (Plate 7, Fig. 4), the dorsal border of which attaches the sinus venosus (Plate 7, Fig. 4). The base of the extension is fused with the lateral body walls, forming the cranial component of the wall of the abdominal coelom, hereinafter referred to as the septal wall (Plate 7, Fig. 4). The remainder of the extension is a tongue-shaped structure ventral to the pericardium (Plate 8, Fig. 1), to which it is fused in the median plane immediately cranial to the septal wall: in the interest of easy reference the term septal fold is introduced.

The amnion as in E346 is attached to the cranial and lateral margins of the fold; from the latter the amnion is reflected directly to the lateral folds. The area of fusion of yolk sac splanchnopleure with septal fold and amnion, described in E346, is mobilized to form a broad suspensory ligament (Plate 7, Fig. 4; Plate 8, Fig. 1), continuous with the ventral mesentery and extending over the surface of the septal wall, the septal fold, and the amnion. The amniotic portion of the ligament is prolonged to the cranial limits of the embryo, and is referred to subsequently as the vitello-amniotic ligament (Plate 9, Fig. 2; Plate 10, Figs. 3 and 4).

The allantois is a curved cylindrical mass, lying to the right of, and dorsal to, the caudal third of the embryo (Plate 4, Fig. 2); its dorsal surface is adherent to the chorion (Plate 4, Fig. 2). Translocation from the original ventral position is associated with growth and torsion in the caudal region of the embryo: the cloacal region has overgrown the allantois, torsion has rotated to the right the caudal third of the embryo together with the attached allantois (Plate 7, Fig. 3), the splanchnic stalk passes caudally to enter the allantois on the right side of the body (Plate 7, Fig. 3). The umbilical arteries flank the allantoic duct, the left artery cranial, the right caudal. The left umbilical vein, which is cranial to the corresponding artery, enters the left embryonic rim by passing transversely across the ventral surface of the embryo (Plate 7, Fig. 3); the right umbilical vein is caudal to the corresponding artery. This vascular relationship is maintained during the embryonic and foetal periods: the umbilical vessels of the left side ramify in the cranial, those of the right side in the caudal region of the allantois. Histologically the allantois is a dilated endodermal tube, walled by dense avascular haemopoietic tissue (Plate 7, Fig. 4; Plate 8, Figs. 2 and 3) in continuity with the intravascular haemopoietic tissue of the umbilical veins.

Group II (6–6·9 mm).—Group II includes four embryos, E340, E325, EX, and ESN45, all of which are sectioned serially. E340 has the smallest chorionic vesicle (105 mm overall) of Groups I and II, whilst ESN45 has the largest (220 mm). Maceration rendered differential staining of E340 inadequate.

The cellular allantois of Group I is superseded by a membranous sac, partially fused with the chorion, forming an allanto-chorion (Plate 4, Figs. 3 and 4). The dorsal mesentery is lengthened, and the midgut is delimited from the yolk sac by a vitello-intestinal portal. Caudal to the liver the lateral body walls are thickened and deepened, incorporating the umbilical veins; lateral folds attach the amnion. In embryos of Group II the septal fold is cardiac in position and is in continuity with the cardiac lamina of the septum and the ventral pericardium (Plate 9, Fig. 1). Fore limb buds are represented by mesodermal elevations ventral to the somites and lateral to the pleuro-peritoneal passages, into which the lung buds project. The characteristic growth change of this group is caudal elongation whereby the cloacal region is recurved ventrally and to the right in E340, E325, and ESN45, and dorsally in EX. Specimens illustrating the group are E325 and ESN45 (Plate 1, Figs. 3 and 4).

In E325, in the loop joining the distal and proximal limbs of the recurved region, the dorsal mesentery and mesonephroi end, the aorta divides, and the umbilical arteries enter the distal limb ventral to the allantoic duct. Flanking the arteries the umbilical veins lie in the body wall, completing the assembly of the allantoic stalk. The lateral folds contribute mesodermal extensions on either side of the stalk; passing dorsally between the limbs of the caudal loop, the stalk reaches the allantoic sac, dorsal and caudal to the embryo (Plate 4, Fig. 3). The stalk mesoderm ensheathes the umbilical vessels as they course cranially and caudally on the surface of the allantoic sac. Folds project into the allantoic cavity from the dorsal wall: the chorion does not participate in the folding, but is fused with the allantois in the areas of apposition.

The blood vessels are distended with cells in haemopoiesis. The midgut lumen is in the form of a longitudinal cleft, sheathed by mesoderm which is in continuity with the dorsal and ventral mesenteries (Plate 8, Fig. 4). The caudal two-thirds of the gut lies in the extraembryonic coelom where it communicates with the yolk sac by means of an elongated vent (Plate 8, Fig. 4). The caudal half of the gut sheath is ridged by branches of the mesenteric artery (Plate 8, Fig. 4); the sheath is continued over the proximal wall of the yolk sac, a continuity which is sustained in later embryos after the disappearance of the vitello-intestinal duct. The yolk sac disperses cranially and caudally from the vitello-intestinal junction, the contiguous cranial region is attached to the septal wall and septal fold by the suspensory ligament, and to the amnion by the vitello-amniotic ligament. The patent chorio-amniotic ligament is 3 mm in length (Plate 4, Fig. 3).

EX is a well-preserved embryo, providing adequate histological detail. It is unique in the series in that the allantois is ventral and left-sided to the embryo, the yolk sac is on the right side and dorsal, a reversal of membrane disposition (Plate 4, Fig. 5). The flexion of the cloacal region is dorso-caudal in the median plane, forming an S-shaped embryo; torsion of the distal limb brings the ventral surface to the right. The allantois is folded and lobulated; distended haemopoietic cords are a feature of the vascular pattern (Plate 4, Figs. 5 and 6). EX appears to be a healthy variant: the issue of viability is contingent upon a suitable mechanism for the assembly of the umbilical coelom and the closure of the body cavity; if such a mechanism exists, its mode of action is not apparent. The position of the chorio-amniotic ligament in relation to the chorion suggests a rotation of the embryo through 180° at a stage prior to chorio-allantoic fusion. The allantoic stalk is assembled as in the other embryos of the group.

ESN45 has a caudal disposition similar to that of E325, except that the loop device is extended to form a complete gyre of an open spiral; the ventral surface of the distal limb faces caudally, whilst its free end reaches beyond the dorsal surface of the embryo in the midgut region (Plate 8, Fig. 5). The allantoic stalk in its assembly and form is as described in E325; its relation to the embryo is confined to the ventral surface of the cloacal region from which it arises (Plate 8, Fig. 5). The allantois is a fluid-free sac as in other members of the group, but whereas the redundancy of surface area in E325 and EX is expressed in folding and lobulation, in ESN45 there is a complete invagination of the allantoic wall from the dorsal surface, outer and inner walls being closely approximated (Plate 8, Fig. 5); the chorion is not involved, but is in part fused with the outer wall of the sac. The midgut has assumed the tubular form, the cranial limb is attached by the ventral mesentery to the caudal surface of the liver; in the dorsal mesentery two large branches of the superior mesenteric artery are associated with the caudal limb; at the site of the midgut loop the lumen is expanded to form a tubular junction with the yolk sac. The mesodermal gut sheath is continued over the yolk sac carrying the branches of the mesenteric artery. The proximal tubular region of the yolk sac is attached by the suspensory ligament to the septal wall and septal fold (Plate 9, Fig. 1). The vitello-amniotic ligament is the site of cranio-caudal prolongation of the yolk sac (Plate 9, Fig. 2); it extends from the caudal pharyngeal arches to the vertex of the forebrain vesicle. In the abembryonic areas of the yolk sac the vascular splanchnopleure is remarkable for the distension of the longitudinally disposed blood vessels and for a series of longitudinal ridges projecting into the exo-coelom (Plate 9, Fig. 3). Coagula of the type illustrated in the exo-coelom of ESN45 (Plate 9, Fig. 2) are present also in the allantoic sac in older embryos. Calculated from the sections, the length of the tubular chorio-amniotic ligament is approximately 5 mm; the trophoblast contiguous with the chorionic attachment is a circumferential area of large vacuolated epithelial cells adherent to the chorion (Plate 9, Fig. 3), elsewhere the trophoblast has been shed.

Group III (7–7·9 mm).—Group III is represented by E371, 7·5 mm in length. Field notes record a lapse of 24 hours between killing and flensing, and degeneration of the uterine mucous membrane; despite maceration, the embryo shows satisfactory morphological detail. The elongated form of the chorionic vesicle of the earlier embryos is modified in E371 by enlargement and fluid distension of the allantoic sac, the undilated portions of the vesicle appearing as caudal and cephalic extensions of the expanded region of the allanto-chorion; the respective lengths of these processes are 94 mm and 67 mm, the former terminating in a vesicle and the latter in a filament (Plate 1, Fig. 5). Head–tail length of the allantois is 17 mm. The caudal spiral arrangement described in ESN45 is resolved in E371 by absorption of the region proximal to the cloaca (and inclusive of the root of the allantoic stalk) into the general dorsal curvature. The terminal part of the embryo, including cloaca and the attenuated anlage of the tail, is flexed ventrally (Plate 5, Fig. 1). Caudal growth of mesonephroi and of the dorsal mesentery extends the coelom as far as the cloaca, segregating the allantoic duct and associated umbilical arteries in the ventral coelomic wall, which is continuous with the root of the allantoic stalk (formed by the duct and arteries closing the interval between, and fusing with the lateral body walls) (illustrated in Group IV by Plate 10, Fig. 3); the stalk passing dorsally lies parallel to the right flank of the embryo (Plate 5, Fig. 1). The amniotic cul-de-sac investing the ventral cloaca-tail region is attached to the lateral folds which are reflected on their respective sides from the stalk close to the root. The mesodermal portion of the stalk is derived from the prolongation of part of the lateral body walls, the contribution of the left lateral body wall passes ventral to the embryo. Resulting from bifurcation of the umbilical arteries in the root of the stalk, four arterial stems accompany the allantoic duct; entering the distal attachment of the stalk are four umbilical veins, of which the two cranial join to form the left, and the two caudal to form the right umbilical vein: this variation is peculiar to E371. The mesoderm of the stalk is prolonged over the surface of the allantois forming a sheath for both cranial and caudal umbilical vessels. The vitello-intestinal junction is tubular, the lumen appreciably diminished compared with that in ESN45. Furthermore the tubular stalk of the yolk sac is markedly reduced in calibre, not only in the region of its attachment to the septal fold, but also where it is attached to the amnion by the vitello-amniotic ligament, thus providing a yolk sac pedicle, which is on the left side of the embryo, whereas the allantoic stalk is on the right, a relationship maintained throughout the embryonic period. Caudal growth of the liver has extended the septal wall over its ventral surface, resulting in the separation of septal fold from the septum transversum and the pericardium; the septal fold lies ventral to the liver.

Group IV (8–8·9 mm).—Group IV is represented by three embryos, E274 (8·2 mm), E267 (8·7 mm), and E288 (8·9 mm); E274 and E267 were in a recent state when collected, providing critical histological material; E288, although macerated, contributed morphologically.

Respective measurements of the cranial and caudal chorionic processes are E267, 78 mm and 92 mm (Plate 1, Fig. 6) and E288, 100 mm and 110 mm. In E267 the allantoic sac, which is partially inverted and has an excess of chorion in the allanto-chorion (Plate 11, Figs. 1 and 5), is 25 mm in length; that of E288 is 40 mm. E267 was sectioned with membranes intact. E274 en route from uterus to formalin dropped on the flensing deck, fortuitously providing through the ruptured membranes an unrestricted view of the embryo and its unusual adnexa (Plate 5, Fig. 3); measurements other than that of the embryo and of the chorio-amniotic ligament are invalid.

The cloacal region is aligned in the overall dorsal curvature of the embryo. The allantoic stalk is in the definitive ventral position deviating to the right (Plate 5, Fig. 3); it lies caudal to the pedicle of the yolk sac which deviates to the left (Plate 5, Fig. 2). In E274 the tail anlage is small and recurved (Plate 5, Fig. 2), whereas in the older embryos of the group it is prolonged in the arc of dorsal curvature reaching the ventral level of the cardiac bulge (Plate 11, Fig. 4). In the cloacal region the post-anal gut persists and metanephric buds are present; lateral to the cloaca hind limb buds appear as mesodermal elevations (Plate 5, Fig. 3). Both vitelline veins are present in E274 (Plate 10, Fig. 1), the right vein being smaller than the left; in E267 the right vein is lacking (Plate 9, Fig. 5), the portal system superseding the omphalomesenteric anastomosis. An elongated patent vitello-intestinal duct connects the cranial limb of the midgut with the yolk sac pedicle in E267 (Plate 9, Fig. 4); a reduced attenuated duct is present in E274; gut and yolk sac are discrete in E288. Beyond the midgut loop, the gut sheath containing the vitelline artery is continued over the caudal wall of the yolk sac pedicle at its attachment to the septal fold (Plate 9, Fig. 6); the pedicle proceeds to the yolk sac from its amniotic attachment (Plate 11, Fig. 4). In E267 the vitello-amniotic ligament is short, terminating over the cardiac bulge (Plate 11, Fig. 4); in E274 and E288 it extends cranially to the level of the telencephalon (Plate 10, Fig. 4). Cervical in position, the heart is more prominent than the liver, which occupies the cranial half of the abdominal coelom; at the caudo-ventral border of the liver the umbilical veins meet in the base of the septal wall to form the ductus venosus, which enters on the left of the gall bladder. The proximal segments of the umbilical veins are patent, continuing in the lateral body walls to the ducts of Cuvier; in E267 and E288 these vessels are much the same calibre as the distal segments. With the caudal growth of the liver, the septal wall extends over its ventral surface. Body walls are deepened and thickened dorso-ventrally; the umbilical veins are situated dorsally in the body wall (Plate 9, Figs. 4 and 5), and the septal fold lies ventral to the liver (Plate 9, Fig. 6); the ventral mesentery is remarkable for its width (Plate 9, Fig. 5). The suspensory ligament attaching the midgut to the septal wall (Plate 9, Fig. 5) is attenuated in contrast to its robust proportions at the attachment to the septal fold (Plate 9, Fig. 6). The lateral body walls, with lateral folds, pass ventrally and caudally from the level of the septal fold to the root of the allantoic stalk (Plate 10, Figs. 1–4). The lateral folds carry the amnion, reflected from the septal fold, to the stalk and its extensions on the allantoic wall (Plate 10, Figs 1–4). The stalk is massive (Plate 5, Fig. 3) owing to the mesodermal content, derived from both body walls and lateral folds (Plate 10, Fig. 4).

In E274 the chorio-amniotic ligament has differentiated into a partially fibrosed avascular tube, 10 mm in length; the amniotic attachment is reinforced by the spread of cellular connective tissue over the contiguous suface of the amnion (Plate 11, Fig. 6). The chorionic attachment, illustrated by E267, is tapered and thicker than the rest of the ligament, and is in continuity with the margin of the allanto-chorion; an external orifice, plugged with vacuolated hypertrophic trophoblast cells, projects from the chorionic surface (Plate 11, Figs. 1 and 3). The chorio-amniotic ligament lies wholly in the extraembryonic coelom (Plate 11, Fig. 2); it consists of fibrosing cellular connective tissue; in subsequent stages it becomes completely fibrosed and the lumen is occluded. Variability is a matter of length.

Trophoblast is found *in situ* over isolated areas of the chorion, allanto-chorion, and trilaminar omphalopleure in E267; histologically it is in the form of a low cubical epithelium with basophilic vacuolated cytoplasm (Plate 12, Fig. 1). Although the distended allantois occupies the greater part of the chorionic vesicle the area of allanto-chorion is restricted; indeed the coelomic surface of the allantois is more extensive. The yolk sac has enlarged; the area of trilaminar omphalopleure exceeds that of the allanto-chorion (Plate 11, Fig. 1). Inherent in yolk sac inversion is the equivalence in area of vascular splanchnopleure and omphalopleure.

In the head region the notochord lies in the median plane, centrally situated in the parachordal mesoderm; dipping slightly ventrally it terminates dorsal to the posterior wall of Rathke's pouch. The membranous labyrinth consists of two vesicles in line and a third lying dorso-medially, connected by a short stalk; the pedunculated vesicle constitutes the ductus endolymphaticus. Rathke's pouch is apposed to the dorsal surface of the diencephalon, at which point it is dorsoventrally compressed. From the ventral surface of the diencephalon the optic stalks project laterally to terminate in shallow optic cups; thickening of the overlying ectoderm represents the anlage of the lens.

Four well-developed arches with corresponding grooves form the pharyngeal wall; the sixth arch is represented by the arytenoid tubercles. The thyroid is a solid epithelial strand in the median plane, terminating in the pericardium. The larynx, surmounted by the arytenoid tubercles, is sealed by a median sagittal raphe. The lung buds, arising from the bifid caudal end of the trachea, project into the pleuro-peritoneal passages.

Group V (9–9·9 mm).—Group V is represented by E248, 9·5 mm in length. Caudal and cephalic chorionic processes measure 112 mm and 100 mm respectively; the allantoic sac is 55 mm in length (Plate 2, Fig. 1). The most conspicuous feature of this embryo (viewed through the membranes) is the large tail recurved ventrally, the tip lying close to the forebrain vesicle (Plate 14, Fig. 4). E248 is sectioned in its investing membranes.

Dorsoventral deepening of the septal wall has lifted the septal fold away from the liver area to lie over the cardiac bulge. The root of the allantoic stalk is now dorsal to the septal fold. The lateral body walls are entirely fused with the proximal part of the stalk, forming a tube containing the midgut and the vitelline vein. The lumen of the tube is bounded cranially by the septal wall, from which the midgut and vitelline vein are suspended, and laterally and caudally by the conjoined body walls and allantoic stalk (Plate 13, Figs. 1, 2, and 3). Patent at both ends, the tube connects the abdominal coelom with the extraembryonic coelom at the level of the septal fold (Plate 13, Figs. 3 and 4). The distal part of the allantoic stalk is projected from the caudal wall of the tube to join the allantoic sac (Plate 14, Figs. 2–4), The amnion is reflected from the lateral margins of the septal fold to the stalk, and then, as in embryos of Group IV, becomes attached by the lateral folds to the extensions of the stalk on the allantoic wall (Plate 13, Fig 4; Plate 14, Figs. 1–4). Ventral to the septal fold the midgut projects from the lumen of the tube into the extraembryonic coelom (Plate 14, Fig. 1), the gut sheath spreading over the caudal region of the yolk sac pedicle (Plate 14, Fig. 2). The vitelline vein passes into the tube in the suspensory ligament (Plate 13, Fig. 4), and the vitelline artery, enveloped in mesoderm of the gut sheath, passes to the yolk sac pedicle at the level of the midgut loop (Plate 14, Fig. 1). Subsequently the midgut loop retracts into the lumen of the tube, where intestinal growth by coiling proceeds. Attenuation of the ventral mesentery distal to the gastroduodenal region and of the suspensory ligament attached to the septal wall is the prelude to disappearance (Plate 12, Figs. 3 and 4; Plate 13, Fig. 1); that part of the suspensory ligament attaching the yolk sac pedicle to the septal fold is retained throughout the embryonic period.

In the head region ventral to the diencephalon and cerebral vesicles, broad shallow olfactory pits and an extensive fronto-nasal field form a prominent area (Plate 13, Fig. 4). As in Group IV the notochord is central in the parachordal mesoderm, and ends immediately dorsal to a wide open Rathke's pouch. The anlage of the internal ear and ductus endolymphaticus is tubular in form and remarkable in extent. The optic cups are lateral to the diencephalon and dorsal to the olfactory pits (Plate 14, Fig. 2); the lens vesicles are free and lie in the margins of the cups.

The lung bud pattern shows primary branching including an eparterial bronchus. The first and second pharyngeal arches are visible externally and internally; differentiation has obliterated the third and fourth arches. The ducts of Cuvier are suspended in the free margins of the pleuro-peritoneal ligaments; the coelomic cavities intercommunicate. The arytenoid tubercles project cranially to the roof of the pharynx. Gonads are present. Organogenesis in E248 corresponds to that of other mammalian embryos of similar size.

Group VI.—This group comprises three embryos; E240 and E282, both 15 mm in length, and E1A, 15·5 mm (Plate 2, Fig. 2). Measurements of the caudal and cephalic chorionic processes are 130 mm and 137 mm for E240, 125 mm and 43 mm for E282, 78 mm and 85 mm for E1A; the allantoic sacs are 74 mm, 82 mm, and 80 mm respectively. In E240 the pericardial, pleural, and peritoneal cavities and the umbilical coelom are distended by haemorrhage, resulting from rupture of the ductus venosus at the site of entry to the liver.

There is close correspondence in the external features of the three embryos. The head is at right angles to the body. Bounded by maxillary and mandibular mesoderm, the mouth is prominent. Both fore and hind limbs point caudally; the fore limbs (orientated in the permanent dorsoventral axis) are elongated and paddle-shaped, contrasting with the smaller peg-like hind limb buds; a bilateral thickening, the milk line, extends between the limbs. No external trace of somites remains. The tapered tail continues in the arc of dorsal curvature of the embryo, its ventral surface follows the curve of the milk lines. The liver forms a prominent dome-shaped mass, over which arches the umbilical tube (Plate 5, Fig. 4); the midgut lies in the caudal part of the tube, enlarged by the first coil; the cranial end is occupied by the gut sheath and the vitelline vessels. Attachments and relations of the septal fold remain unchanged. The mesodermal extensions of the allantoic stalk containing the vessels are aligned with the ventral surfaces of the head and tail, the caudal extensions being thicker than the cranial (Plate 5, Fig. 4).

Growth of the allantois has greatly increased the size of the chorionic vesicle; the sac is sausage-shaped with tapered recurved ends which project into the proximal dilated regions of the chorionic processes; the allanto-chorion is smooth and transparent, and restricted in extent by the extraembryonic coelom. Growth of the yolk sac continues (Plate 2, Fig. 2). The chorio-amniotic ligament is fibrosed, its lumen obliterated; in E1A it measures 45 mm (Plate 2, Fig. 2), in E282, 35 mm (Plate 5, Fig. 4).

Development of the axial and fore limb skeleton is in the prechondral stage. In the basis cranii differentiation is evident in the parachordal mesoderm, where a prechondral condensation, representing the basal plate, envelops the notochord and extends ventrally to Rathke's pouch. Dorsolateral to the basal plate are the auditory capsules, the cochlea antero-medial, and the ductus endolymphaticus dorsal to the canaliculi. Rathke's pouch, wide open to the buccal cavity, is flattened dorsoventrally and apposed to the dorsal surface of the diencephalon; an infundibular outgrowth overhanging the pouch dorsally is flanked by cornua forming the pars tuberalis. Lateral to the pituitary the internal carotid arteries enter the brain capsule; ventral to the pituitary the optic stalks deviate dorsolaterally. Pigment granules are present in the bases of the choroidal cells: eyelids are lacking.

The maxillary processes have fused with the nasal, and have invaded the fronto-nasal field. Thickenings of the wall of the cerebral vesicles indicate the site of the olfactory bulbs: dorsal to the olfactory fossae, nerve fibres are distinguishable.

Large arytenoid tubercles extend the glottic raphe to the roof of the pharynx; the laryngeal aperture is closed. Pericardial, pleural, and peritoneal cavities intercommunicate. The right limb of the bifid aorta is the smaller. The bursa omentale has formed dorsal to the stomach, which is two-chambered. The ventral mesentery is retained only in the pancreatico-duodenal region; its hepatic portion has disappeared without trace, as has also the suspensory ligament of the septal wall. Distal to the duodenal region the vitelline vein lies freely in the abdominal cavity and the umbilical coelom (Plate 15, Fig. 3). The gall bladder–bile duct anlage remains undifferentiated. The ductus venosus is formed ventral to the subhepatic notch, between the margins of which the midgut projects into the umbilical coelom and the vitelline vein enters the abdominal coelom. In the embryos of this group the lumina of the vitelline veins are partially occluded by vascular connective tissue derived from the intima (Plate 15, Fig. 3).

Group VII.—This group consists of three embryos: ESN51, 23·6 mm, ESN46, 27 mm, and ESN57, 30 mm. ESN51 and ESN57 were collected in a recent state with membranes intact (Plate 2, Figs. 3 and 4). In ESN46 the membranes were ruptured; the embryo, although shrunken and macerated, provided satisfactory sections. Respective measurements of the allantoic sac of ESN51 and of ESN57 are 126 mm and 166 mm; caudal and cephalic chorionic processes in ESN51 are 166 mm and 153 mm, corresponding measurements in ESN57, 80 mm and 30 mm (Plate 2, Figs. 3 and 4). In ESN51 the yolk sac has retracted from the chorionic processes, extending 50 mm into the caudal, and 65 mm into the cephalic process; in ESN57 allantoic growth has reduced the chorionic processes, and the yolk sac and allantois are of equal length (Plate 2, Fig. 4); in both specimens the extraembryonic coelom has increased (Plate 2, Figs. 3 and 4).

External features common to the embryos of the group are characteristically cetacean (Plate 5, Fig. 5; Plate 6, Figs. 1 and 2). The beak is formed by an extension of maxillary mesoderm and a central paraxial rostrum; the external nares are situated at its base. Elongated fore limbs, with defined digital skeletal areas, are aligned laterally with the mandible. The vertex of the head is the midbrain; the large hindbrain is dorsal; the cerebral vesicles form a frontal bulge.

In ESN51 and ESN46 the base of the umbilical tube lies between the liver and the root of the phallus; the tube arches over the liver to join the septal fold (Plate 5, Fig. 5). In ESN57 the liver mass extends to the root of the phallus, the attachment of the umbilical tube is placed over the subhepatic notch ventral to the liver; the tube, lying parallel to the ventral body wall, passes cranially to join the septal fold (Plate 6, Fig. 2). The chorio-amniotic ligament is 65 mm in ESN57 (Plate 6, Fig. 2); in ESN51 the ligament (30 mm) is adherent in its distal third to the allantois (Plate 5, Fig. 5).

The development of the chondrocranium is expressed in mesenchymal condensations, prechondral and chondral stages. The basal plate and associated occipital arches are cartilaginous. At the anterolateral end of the plate chondral extensions (laminae supracochleares) arch over and blend with the medial margins of the cochlear region of the auditory capsule. The notochord enters the basal plate from the tip of the odontoid peg, is centrally situated for a short distance, then emerges on its dorsal surface; at the base of the laminae supracochleares it is again encapsulated, but reaches the surface with a right-angled bend. After a second equally abrupt turn, the notochord proceeds on the surface between the laminae to terminate immediately dorsal to the pituitary anlage. A cartilaginous basisphenoid attaches slender chondrified alae temporales, the tips of which lie medial to the mandibular division of the trigeminal nerve. An epithelial strand embedded in the basisphenoid connects the pituitary with the roof of the buccal cavity. The cranial surface of the basisphenoid is flat, lacking sella turcica and pituitary fossa. Orbital cartilages extend as horizontal plates to the lateral cranial walls. The chondral nasal septum is continuous with the presphenoid and is prolonged as the rostrum almost to the tip of the beak. The nasal capsule is lateral to the upper region of the nasal cavities; posteriorly on either side it is united to the orbital cartilages by slender prechondral laminae orbito-nasales. Posterior to the nares cartilaginous extensions of the capsule fuse with the nasal septum at the base of the beak, overlying the olfactory nerves. A ventral extension of the capsule on either side of the rostrum represents the anlage of the cartilago ductus nasopalatini. The external nares are paired crescentic slits, the concavities directed ventrally. The olfactory bulbs are well developed, their cavities in continuity with those of the cerebral vesicles. The olfactory nerve fibres form large compact bundles arising from the epithelium of the medial walls of the upper region of the nasal fossae; the latter open widely into the buccal cavity. The palatal processes are lateral to the tongue mass; labio-gingival grooves are present in upper and lower jaws. Eyelids, upper and lower, are represented by slight folds; the lens fibres are differentiating. The auditory capsule is a mesodermal condensation with a prechondral zone along its ventral wall; semicircular canals have differentiated in the canalicular portion which is lateral to a large cochlear. The jugular foramen transmits the last four cranial nerves lying medial to the internal jugular vein; hypoglossal foramina are absent. Reichert's cartilage, completely chondrified, is attached dorsally to the auditory capsule medial to the seventh nerve, forming the tympano-hyal; the remainder of the cartilage, the stylo-hyal, has a mesenchymatous attachment to the basi-hyal on either side of the median plane. Meckel's cartilage, arising between the meatal plate and the tubotympanic recess, is chondrified except at the symphysis; both Meckel's and Reichert's cartilages are bent into a series of curves. In the pharyngeal region the epiglottis is recurved, the tip lying cranial to the arytenoid tubercles; ary-epiglottic folds are present. Two cartilage nodules lie at the base of the vestigial hind limb (Plate 15, Fig. 1).

Dedifferentiation of the tubular gall bladder–bile duct anlage is expressed in discrete clusters of epithelial cells in all embryos of the group.

The blood vascular system is described under three headings: rete, arteries, and veins.

Rete.—Developing connective tissue regions of the embryos of Group VII are beset with sinusoids of variable form and size, which coalesce and are drained by large veins converging on the caval trunks. The histology appears to be a network of anastomosing arterioles which open directly into the sinusoids; this constitutes the rete system of the embryo.

In the central nervous system the rete is formed in the pre-meningeal tissue. In the vertebral canal the blood supply is from the intercostal and vertebral arteries; the venous drainage is by longitudinal channels, ventral to the anterior nerve roots, entering the dorsal thoracic vein at the level of the neck of the first rib; the sinusoids are most prevalent ventral to the spinal cord. In the cranial cavity the internal carotid arteries supply an extensive network in the cleft between the hindbrain and the diencephalon; vertebral arteries do not enter the cranial cavity; venous drainage is by the internal jugulars.

Smaller rete areas are present in the maxillary and mandibular mesoderm. In the cervical region the efferent vessels enter a large transverse cervical vein (Plate 15, Fig. 2). The lateral thoracic vein, which receives the axillary, drains a similar system in the lateral thoracic wall (Plate 15, Fig. 2); in its proximal portion the vein is homologous with the subclavian. Caudally a lumbar rete connects with the inferior vena cava.

Arteries.—The aortic arch and its definitive branches are established. The first is the innominate artery which divides into right common carotid and subclavian; after giving off the internal mammary and dorsal thoracic, the subclavian is continued as the axillary, which supplies branches to the cervical and lateral thoracic rete. On the left side the common carotid arises directly from the aortic arch; both common carotids terminate by dividing into internal and external branches, the latter supplying the rete of the mandibular and maxillary regions. The left subclavian and dorsal thoracic arteries arise close to one another from the terminal part of the aortic arch. The ductus arteriosus joins the aorta between the origins of the subclavian and the common carotid. The left subclavian gives off the internal mammary and continues as the axillary; it also sends branches to the cervical rete; the axillary supplies the lateral thoracic rete. The small vertebral arteries are branches of the dorsal thoracics.

At the site of bifurcation of the aorta the caudal artery proceeds in the median plane ventral to the vertebrae; at the level of the intervertebral disks it is arched by the cartilage models of the chevron bones (Plate 15, Fig. 1); it supplies the caudal region, and presumably later the fluke.

The umbilical arteries, after giving off large inferior epigastric branches, become aligned on either side of the allantoic duct in the base of the umbilical tube; in this region the duct and arteries are suspended in mesenteries, the duct projecting between the margins of the subhepatic notch (Plate 15, Fig. 1).

Veins.—The inferior vena cava is formed by the ventral and lateral caudal veins; it receives visceral branches, then enters the liver, where it is joined by the ductus venosus and hepatic veins.

The left innominate is formed by the union of the internal jugular and the dorsal thoracic; it receives the left lateral thoracic and the left transverse cervical; as it arches over the trachea it is associated with the thymus gland, and to the right of the trachea is joined by the right transverse cervical; passing dorsally it unites with the right innominate to form the superior vena cava. Tributaries of the right innominate are the dorsal thoracic, internal jugular, and lateral thoracic veins. All veins entering the innominate complex are channels draining rete areas.

The vitelline vein in ESN51 and ESN57 is of large calibre, distended with blood (Plate 15, Fig. 1); in ESN46 its lumen is occluded by cellular connective tissue.

IV. Description of Foetuses: External Features, Membranes, and Cord

Foetus SN48.—This foetus (63 mm) is complete with membranes; the allantoic sac (290 mm) had been opened in the field, exposing the foetus (Plate 3, Fig. 1). The cephalic chorionic process measures 85 mm, the caudal 25 mm. In the foetal region the extraembryonic coelom is obliterated by a vascular allanto-amnion, involving most of the amniotic sac (Plate 3, Fig. 1, and Plate 6, Fig. 3), except on the left ventral aspect of the foetus, where the coelom is closed by an area of chorio-amnion vascularized by branches of the allantoic vessels. Other than where attached to the extensions of the umbilical cord, the allanto-chorion is thick and opaque, owing to mesodermal increments. The entire amniotic sac has invaginated the allantois. A short stout umbilical cord, formed by the fusion of septal fold and allantoic stalk, is continuous with the mesodermal extensions, which attach on the right by a common ligament the allanto-chorion and the allanto-amnion, and on the left the chorio-amnion (Plate 15, Fig. 5). The umbilical cord, the allantoic duct, and the extensions of the cord are detached from the wall of the allantois, and are fused ventrally with the chorion; the extensions are fused dorsally with the amniotic sac. Constrictions in the allanto-chorion caudal and cephalic to the extensions of the cord obliterate the allantoic cavity; in these regions the umbilical vessels pass to and from the horizontally opposed cord extensions (Plate 3, Fig. 1). The allantoic duct is large and widely patent in the proximal part of the cord; in the distal part its lumen is slit-like (Plate 15, Fig. 5); in the terminal region of the cord the duct widens to form an elongated vent open on the chorionic surface. The allanto-chorion and chorio-amnion are smooth and devoid of folds (Plate 3. Fig. 1). The chorio-amniotic ligament has disappeared without trace.

The yolk sac is a tubular strand of vascular splanchnopleure in which peripheral distended blood vessels are longitudinally disposed (Plate 15, Fig. 5). It lies along the caudal extensions of the umbilical cord, proximally in the root of the attachment of the chorio-amnion and distally, crossing to the right, it passes into the common attachment of the chorio-amnion and allanto-chorion, where it terminates (Plate 15, Fig. 5).

The rete areas of the foetus are indicated by superficial veins in the cervical, lateral thoracic, and caudal regions. The tail is tapered at its extremity (Plate 6, Fig. 3).

Foetus SN82.—This foetus (90 mm) is severed from its membranes except for a remnant attached to the umbilical cord (Plate 6, Fig. 4). The membrane consists of two layers. The inner, connected with the cord by the allantoic vessels and duct, is ensheathed in amnion reflected from the cord, relationships which identify it as allanto-amnion. The outer layer (allanto-chorion) is beset with branched chorionic villi (Plate 15, Fig. 4); it is apposed to the inner layer by fortuitous folding; the cleft represents allantoic cavity. The cord is more slender than that of FSN48; it terminates by the dispersal of the umbilical vessels, which separate into the usual caudal and cranial groups, signifying that the extensions have been approximated and taken into the distal part of the umbilical cord. The allantoic duct is large and widely patent, both in the cord and where it lies between the paired vessels (Plate 6, Fig. 4) before opening into the allantoic cavity.

The yolk sac is present in the terminal part of the cord; the vascular splanchnopleure is more solid than tubular. The vitelline vessels are patent as in the younger foetus.

The cervical, lateral thoracic, and caudal rete areas are indicated by the associated superficial venous drainage. The tail of FSN82 terminates in a small spatulate fluke (Plate 6, Fig. 4).

V. Discussion

In the previllous phase the membrane surfaces of the embryo and foetus are evenly smooth, whereas the uterine mucosa is arranged in a series of parallel folds and grooves of the order of 25 mm in depth (Plate 3, Fig. 2). The slender elongated chorionic vesicles of the younger embryos are adapted to lie in the grooves, from which some were recovered. Embryos were found in a constant position, indicated by an area of hyperaemia, a correlation suggesting the nidation site. Allantoic growth and distension eventually separates the folds; the unattached vesicle is then free in the uterine fluid (probably this happens in embryos of 10–15 mm, in which the allantoic sac measures from 60 to 80 mm (Plate 11, Figs. 1 and 2)).

Structures which adapt the embryo for immersion in the uterine fluid form a dual suspension of the embryo within the amniotic sac, and a multiple suspension of embryo and amniotic sac in the extraembryonic coelom: with the exception of the chorio-amniotic ligament, these structures are components of the umbilical cord. The suspension, by restricting rotary movement of the amniotic sac and embryo, eliminates torsion of the nutrient vessels. Traction stresses in the vitelline vessels are minimized by the independent attachment of the yolk sac pedicle.

The foetus is adapted against torsion of the umbilical vessels by modification of the embryonic suspension, whereby the foetus and amniotic sac are attached to the cord extensions and immobilized within closely apposed membranes void of allantoic fluid.

In terrestrial mammals, prior to pericardial reversal, the extraembryonic coelom cephalic to the protocardiac area separates the yolk sac splanchnopleure from the amniotic somatopleure; after reversal the splanchnopleure is separate from the amnion, which is attached to the ventral lamina of the septum transversum; the lamina together with the attached amnion forms the cephalic region of the embryonic rim. In *Megaptera nodosa* the separation of somatopleure and splanchnopleure does not occur, so that after heart reversal the yolk sac splanchnopleure is adherent to the coelomic surface of the septum transversum and the attached amnion (Plate 7, Fig. 1), an association expressed in the suspensory ligaments of the gut and yolk sac in Group II embryos. When the gut assumes the tubular form the proximally attached region of the yolk sac is similarly modified (Plate 9, Fig. 1). The splanchnopleuric tube so formed is retained in a cephalic position by attachment to the septal fold and the amnion; it approximates the cephalic and caudal extensions of the yolk sac ventral to the head: ESN45 and E340 illustrate this arrangement (Plate 1, Fig. 4, and Plate 9, Fig. 2). Separation occurs by the growth of the tube ventral to the vitello-amniotic ligament, forming the yolk sac pedicle, begun in Group III and completed in Group IV (Plate 10, Figs. 3 and 4). Provision against traction is in the spongy areolar tissue of the vitello-amniotic ligament, the loosely attached expanse of inverted yolk sac splanchnopleure, and the redundant length of the pedicle. The septal fold secures the pedicle subsequent to regression of the yolk sac and formation of the umbilical cord.

In embryos of Group II the allantois is sustained in the dorsal position by its attachment to the chorion. The allantoic stalk passing dorsally from the cloacal region of the embryo is approximated to the caudal part of the sac by a loop in E325 (Plate 8, Fig. 4) and a spiral device in ESN45 (Plate 8, Fig. 5). The difference between loop and spiral is the measure of elongation of the caudal region of the latter embryo. Growth by invagination of the allantoic sac in ESN45 (Plate 8, Fig. 5) maintains the stalk and the sac in the same relative positions during the attachment of the mesodermal extensions of the stalk to the wall of the sac.

Suspension of the embryo in the extraembryonic coelom begins with the advent of allantoic fluid and is completed by the attachment of the lateral folds to the extensions of the allantoic stalk, The assembly of the anti-torsion device is completed in the 9–10 mm stage by the formation of the umbilical tube, which attaches the embryo within the amniotic sac to septal fold and allantoic stalk.

Occlusion of the lumen of the chorio-amniotic ligament permits the retention of amniotic fluid. The sac is not visibly distended in embryos of Group IV, and if secreted, fluid would leak into the uterine cavity. In the later embryos with a totally fibrosed ligament the amniotic sac is fully distended. Persistent chorio-amniotic connections occur in the oviparous reptiles, birds, and monotremes; in terrestrial mammals in which amniogenesis occurs by folding, the transient union disappears in early somite stages. In *Megaptera nodosa* the chorio-amniotic ligament is functional until the closure of the extraembryonic coelom by the allanto-amnion.

The segregation of the allantoic stalk illustrates the part it plays in the morphogenesis of the umbilical cord; the retarded cord development demonstrates the origin of its components. Sections of the stalk show the inner splanchnic moiety delimited by a membrane, umbilical arteries and the allantoic duct embedded in splanchnic mesoderm (Plate 14, Figs 1 and 2), and an outer somatic mesodermal mass derived from, and for a time in continuity with, body walls and lateral folds (Plate 10, Fig. 4). The lateral folds and septal fold are derivatives of the embryonic rim, destined to maintain its function, namely the attachment of the amnion. The umbilical tube is formed by the base of the allantoic stalk, which incorporates the splanchnic moiety, the lateral body walls, and septal wall (Plate 13, Fig. 2), and becomes the proximal part of the umbilical cord. The lateral folds play no part in the formation of this region of the cord, which is body wall and splanchnic mesoderm.

A striking change is evident in the foetus–membrane complex in FSN48: the compact structure is achieved by a relative reduction in membrane area, thickening of the allanto-chorion, and invagination of the allantois by the amniotic sac. It is not known if fluid was present in the allantoic sac before incision; in view of the reduction of the allantoic cavity and the modification of the allantoic duct for drainage of nephric secretion into the uterine cavity, this would appear improbable. Apparently the mesodermal extensions of the umbilical cord containing the allantoic duct become separated from the allantoic wall during invagination of the sac by amnion and enclosed foetus. As in the embryo, the extensions play the major part in suspension, attaching not only the foetus, but also the entire membrane system, amniotic sac, chorion, chorio-amnion, allanto-amnion, and allanto-chorion. The allanto-amnion, closely applied to the thick walled allanto-chorion, restricts the movement of the foetus within the amniotic sac and provides a strong protective membrane.

In FSN82 it is apparent that the extensions have been taken into the cord by progressive proximal fusion. The manner of reunion of allantoic duct and sac is not demonstrable; implicit in the union is the approximation of the two structures at a stage when the membranes are attaching the endometrium.

The lumen of the proximal segment of the vitelline vein, from being fully patent to totally occluded by connective tissue proliferation of the intima, is variable in embryos within a group. These changes may be correlated with the state of preservation of the specimen: a patent vitelline vein is associated with excellent histological material (characterized by plaques of attached trophoblast and intact yolk sac epithelium). Only this restricted segment of the vitelline vein is affected. Death of the embryo (other than by trauma) would not synchronize with that of the host, and might be delayed, possibly resulting from anoxaemia; during this period the intima proliferates. A similar mechanism operates in the obliteration of effete vessels, a fate which overtakes this segment of the vitelline vein during the final regression of the yolk sac. The stimulus for this mechanism is not known; apparently it is prematurely operative under conditions prevailing in the uterine cavity after death of the host.

Organogenesis corresponds in pattern and in sequence to that of Mammalia of comparable embryo size. In the youngest embryo the neural groove has closed, before the appearance of the pharyngeal arches, which, combined with the broad flat caudal region, renders the form unique. At later stages there is a sequence of specifically cetacean characters, such as absence of belly stalk, wide open abdominal coelom and caudal attachment of the allantoic stalk; these are followed by suppression of hind limb buds, attenuation of the sacral region, elongation of the tail and finally the appearance of the beak. That the embryo and membrane system of an aquatic mammal should so differ from that of the terrestrial suggest that a long period of time separates the Cetacea from other orders.

The development of the blood vascular system conforms to the general mammalian pattern; the outstanding variation is the early appearance of the rete, which adapts the embryo to the differences of pressure experienced during sounding of the maternal host. The internal carotid arteries and the cerebral rete are vessels of the embryo and foetus, replaced after birth by the dorsal thoracic rete and the spinal arteries.

The closed air passage, extending from the external nares to the larynx, is derived from the fused projection of the arytenoid tubercles and the epiglottis.

Development of the long distance receptors proceeds as in land mammals. There are no structural indications of the functional destiny of either smell or hearing. For such a study a series of foetuses is required, the early stages of which might well be filled by the two foetuses of the present collection.

VI. Acknowledgments

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Explanation of Plates 1–15

Plate 1

Embryos in Membranes, Natural Size

Fig. 1.—Group I: E346.
Fig. 2.—Group I: E306.
Fig. 3.—Group II: E325.
Fig. 4.—Group II: ESN45.
Fig. 5.—Group III: E371.
Fig. 6.—Group IV: E267.

Plate 2

Embryos in Membranes

Fig. 1.—Group V: E248. Natural size.
Fig. 2.—Group VI: E1A. Natural size.
Fig. 3.—Group VII: ESN51. ×0·58.
Fig. 4.—Group VII: ESN57. ×0·625.

Plate 3

Fig. 1.—Foetus SN48 in membranes. The cut margins of the allanto-chorion have been widely separated to expose the foetus, exaggerating the extent of the allantoic cavity. ×0·5.

Fig. 2.—Uterine mucosa.

Plate 4

Embryos

Fig. 1.—Group I: E346. Dotted line indicates lateral margin of fusion of vascular splanchnopleure and amnion.

Fig. 2.—Group I: E306. The chorion has been cut away to expose the chorio-amniotic ligament, the area of attachment of chorion to allantois and the ventral attachment of the yolk sac.

Fig. 3.—Group II: E325.

Fig. 4.—Group II: E325 after clearing, showing caudal loop.

Fig. 5.—Group II: EX.

Fig. 6.—Group II: EX after clearing.

Plate 5

Embryos

Fig. 1.—Group III: E371.
Fig. 2.—Group IV: E274.
Fig. 3.—Group IV: E274.
Fig. 4.—Group VI: E282.
Fig. 5.—Group VII: ESN51.

PLATE 6

Embryos and Foetuses

Fig. 1.—Group VII: ESN57. Right side. *c.* × 2.
Fig. 2.—Group VII: ESN57. Left side. *c.* × 2.
Fig. 3.—Foetus SN48 in allanto-amnion. Natural size.
Fig. 4.—Foetus SN82. Natural size.

PLATE 7

Serial Sections

Fig. 1.—Group I: E346. Longitudinal section, sagittal plane.
Fig. 2.—Group I: E346.
Fig. 3.—Group I: E306. Longitudinal section, dorsoventral coronal plane.
Fig. 4.—Group I: E306.
Fig. 5.—Group I: E346. Transverse section, chorio-amniotic ligament.

PLATE 8

Serial Sections

Fig. 1.—Group I: E306.
Fig. 2.—Group I: E306. Transverse section, allantois, from Plate 7, Figure 4.
Fig. 3.—Group I: E306. High power. Allantoic wall, from Plate 7, Figure 4.
Fig. 4.—Group II: E325. Longitudinal section, dorsoventral.
Fig. 5.—Group II: ESN45. Longitudinal section, dorsoventral.

PLATE 9

Serial Sections

Fig. 1.—Group II: ESN45.
Fig. 2.—Group II: ESN45.
Fig. 3.—Group II: ESN45.
Fig. 4.—Group IV: E267. Transverse section.
Fig. 5.—Group IV: E267.
Fig. 6.—Group IV: E267.

PLATE 10

Serial Sections

Fig. 1.—Group IV: E274. Longitudinal section, dorsoventral coronal plane.
Fig. 2.—Group IV: E274.
Fig. 3.—Group IV: E274.
Fig. 4.—Group IV: E274.

PLATE 11

Serial Sections

Fig. 1.—Group IV: E267. $X-Z$, allanto-chorion; $X-Y$, yolk sac; XYZ, extraembryonic coelom. Window see Plate 12, Figure 1.
Fig. 2.—Group IV: E267. Chorio-amniotic ligament.
Fig. 3.—Group IV: E267. Chorionic attachment of chorio-amniotic ligament, from Plate 11, Figure 1.
Fig. 4.—Group IV: E267.
Fig. 5.—Group IV: E267. Chorionic invagination.
Fig. 6.—Group IV: E274. Attachment of chorio-amniotic ligament to amnion.

PLATE 12

Serial Sections

Fig. 1.—Group IV: E267. Redundant chorion (from Plate 11, Figure 1).
Fig. 2.—Group IV: E267.
Fig. 3.—Group V: E248. Dorsoventral, coronal plane.
Fig. 4.—Group V: E248.

PLATE 13

Serial Sections

Fig. 1.—Group V: E248.
Fig. 2.—Group V: E248.
Fig. 3.—Group V: E248. Attachment of septal wall to septal fold.
Fig. 4.—Group V: E248.

PLATE 14

Serial Sections

Fig. 1.—Group V: E248.
Fig. 2.—Group V: E248.
Fig. 3.—Group V: E248.
Fig. 4.—Group V: E248.

PLATE 15

Serial Sections

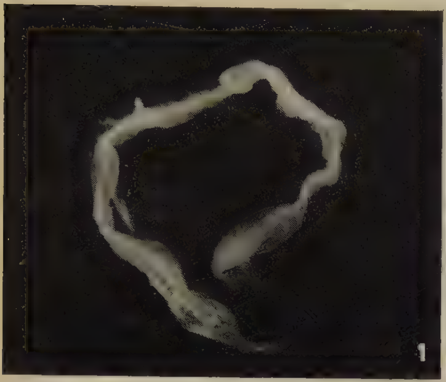
Fig. 1.—Group VII: ESN57.
Fig. 2.—Group VII: ESN57.
Fig. 3.—Group VI: E240.
Fig. 4.—Foetus SN82: Allanto-chorion, villi.
Fig. 5.—Foetus SN48: Junction of cord and extensions and attachment of membranes to the extensions.

LIST OF ABBREVIATIONS IN PLATES

allantois	*al*
allantoic duct	*al d*
allantoic sac	*al s*
allantoic stalk	*al st*
allantoic stalk (splanchnic part)	*al st sp*
allantoic vessels	*al v*
allanto-amnion	*al am*
allanto-chorion	*al ch*
amnion	*am*
amniotic sac	*am s*
basal plate	*b p*
caudal region	*cau*
chevron bones	*c b*
chorion	*ch*
chorionic vesicle	*ch v*
chorionic villi	*ch vi*
chorio-amnion	*ch am*
chorio-amniotic ligament	*ch am l*
coelom	*c*
coelom extraembryonic	*c ex*
coelom umbilical	*c u*
ductus venosus	*d v*
embryonic rim	*e r*
endoderm	*e*
gut	*g*
gut sheath	*g s*
hind limb girdle	*h l*
lateral folds	*l f*
lateral thoracic vein	*l t v*
liver lobe dorsal	*l l*
mesodermal extensions (of allantoic stalk and umbilical cord)	*ext*
midgut	*mg*
midgut loop	*mg l*
omphalopleure trilaminar	*om*
rete cervical	*r c*
rete lateral thoracic	*r l t*
septal fold	*s f*
septal wall	*s w*

septum transversum	*s t*
sinus venosus	*s v*
splanchnopleure vascular	*sp*
suspensory ligament	*s l*
tail	*t*
transverse cervical vein	*t c v*
trophoblast	*tr*
umbilical artery	*u a*
umbilical cord	*u c*
umbilical tube	*u t*
umbilical tube splanchnic part	*u t sp*
umbilical vein	*u v*
umbilical vein left	*u v l*
umbilical vein right	*u v r*
ventral mesentery	*v m*
vitelline artery	*v a*
vitelline vein	*v v*
vitelline veins	*v vs*
vitelline vessels	*v ve*
vitello-amniotic ligament	*v a l*
vitello-intestinal duct	*v i d*
yolk sac	*y s*
yolk sac pedicle	*y s p*
yolk sac tube	*y s t*

EMBRYO AND MEMBRANES OF THE HUMPBACK WHALE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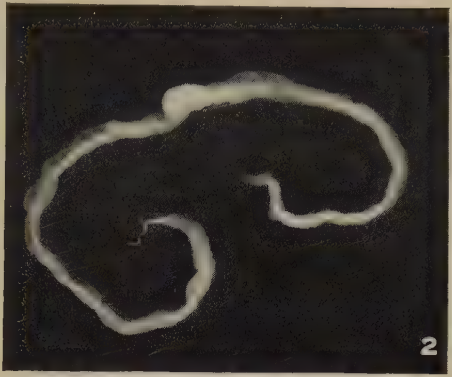
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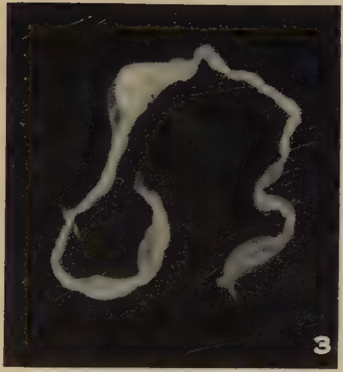
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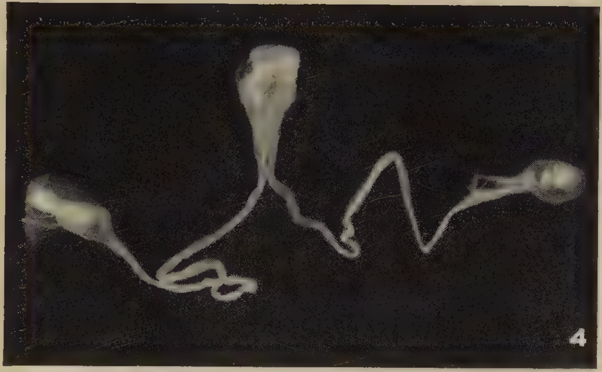
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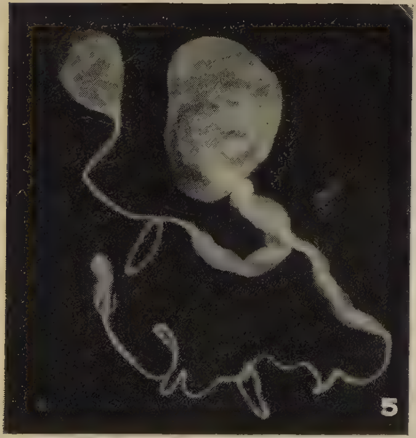
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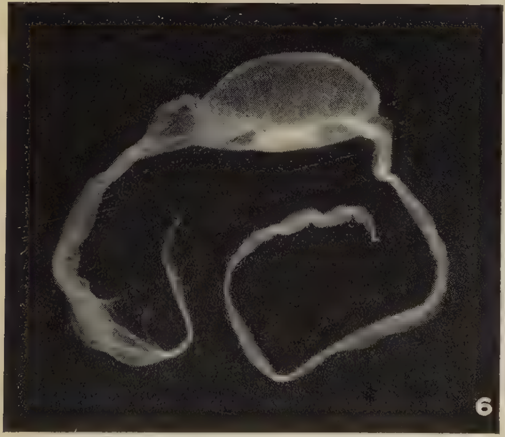
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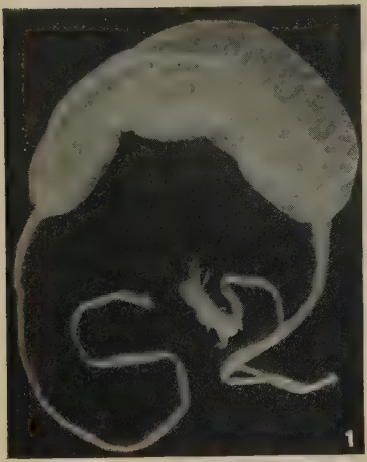

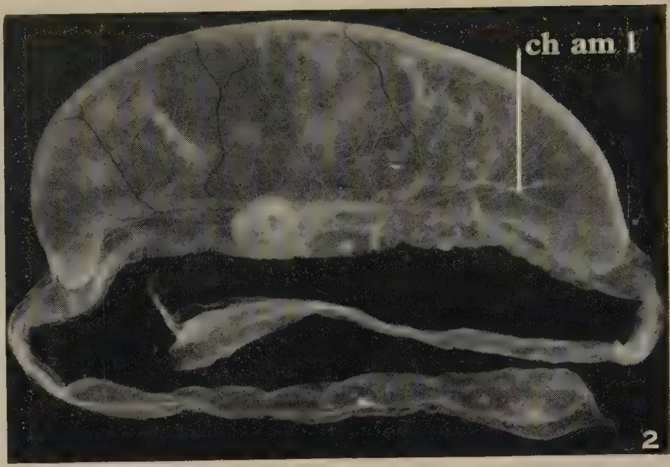

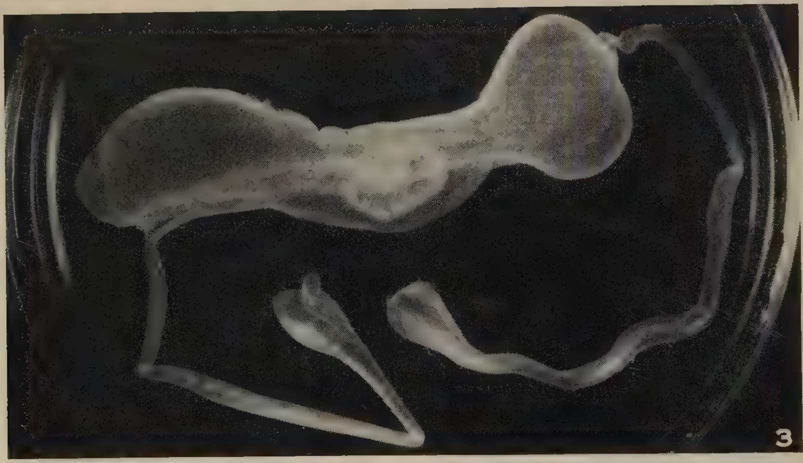

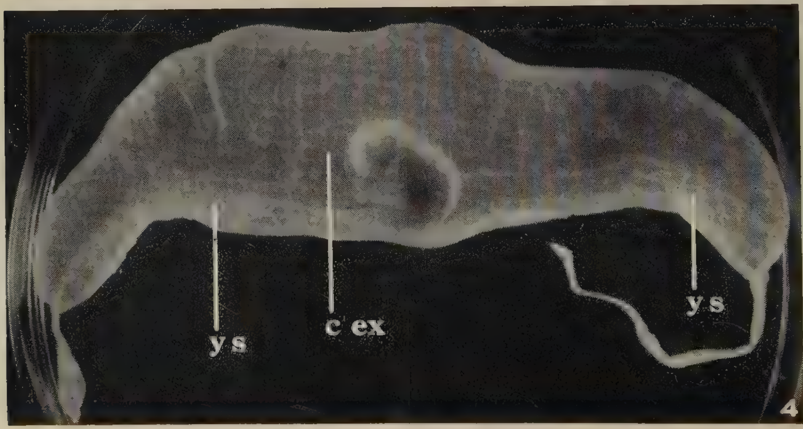

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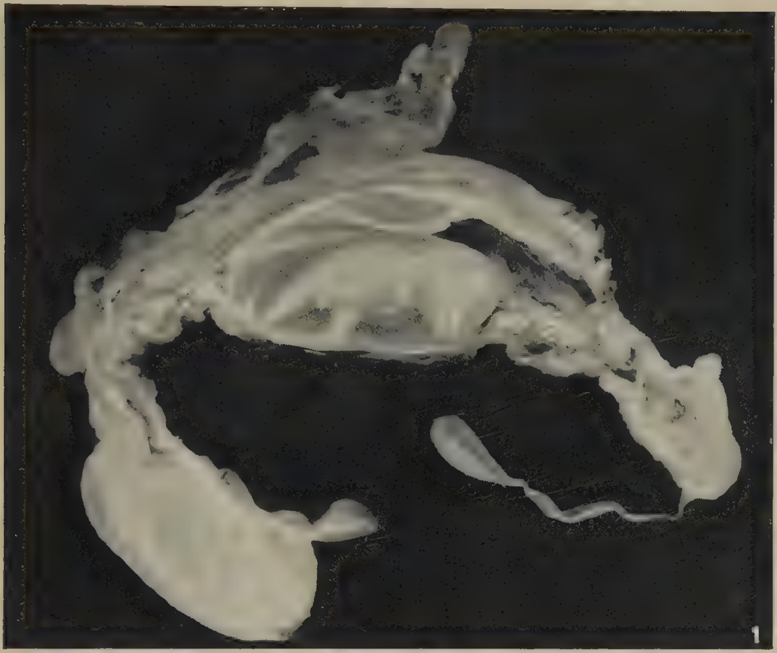
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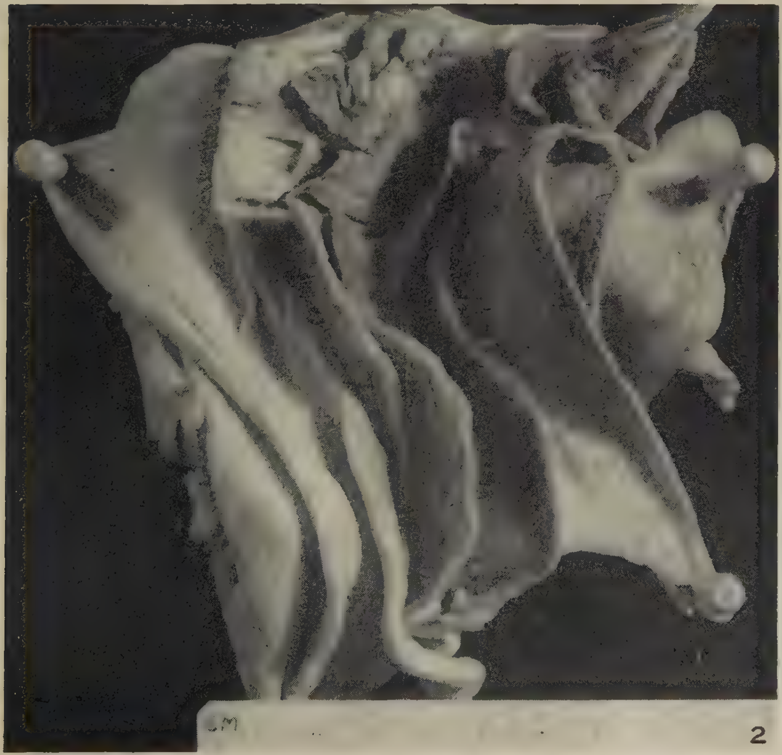

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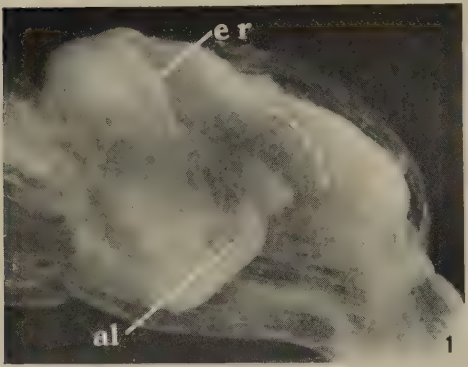

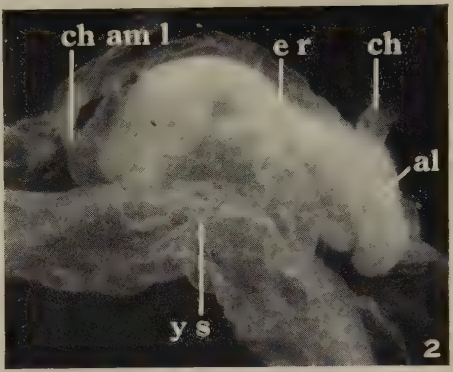
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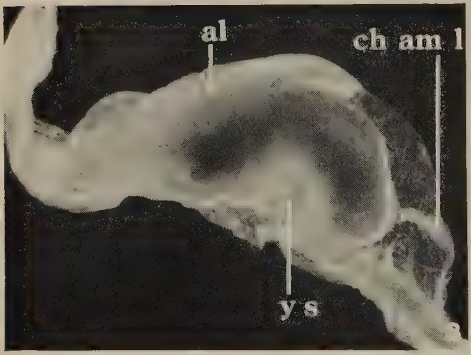

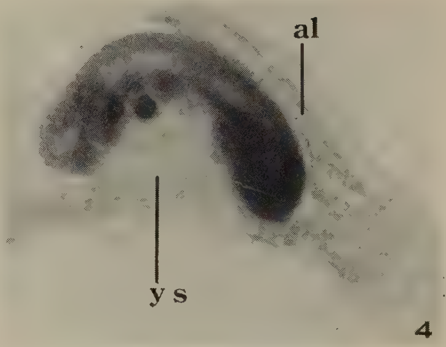

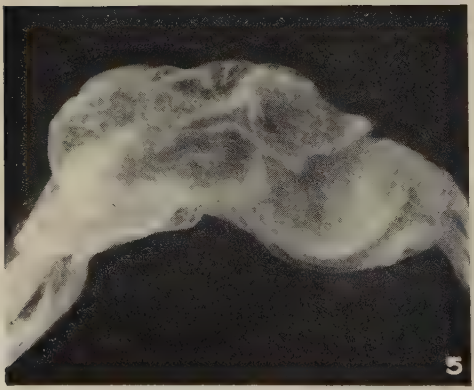

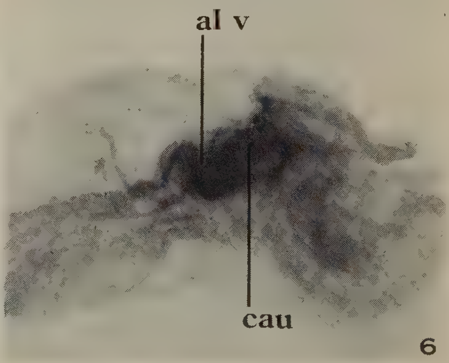

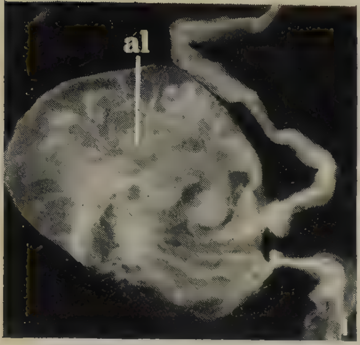
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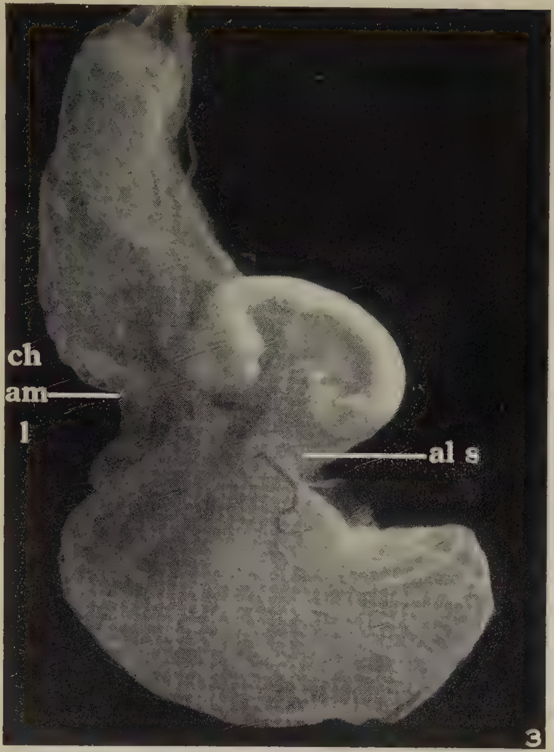
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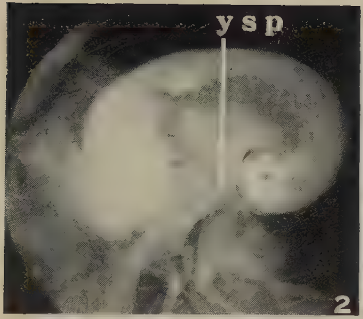
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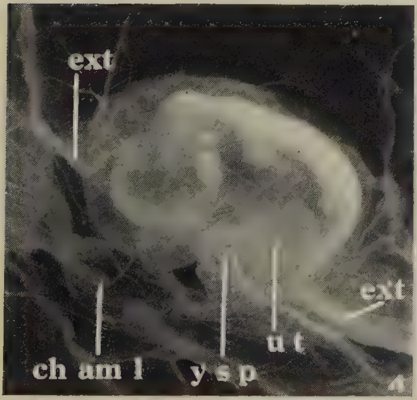
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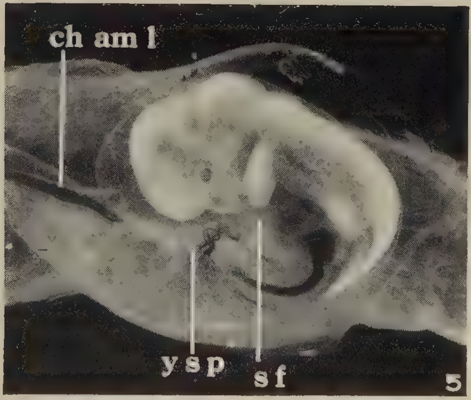
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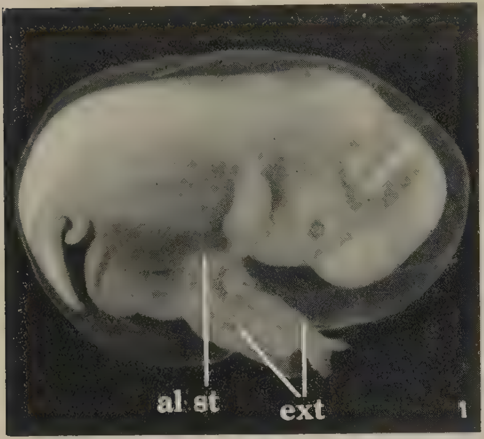
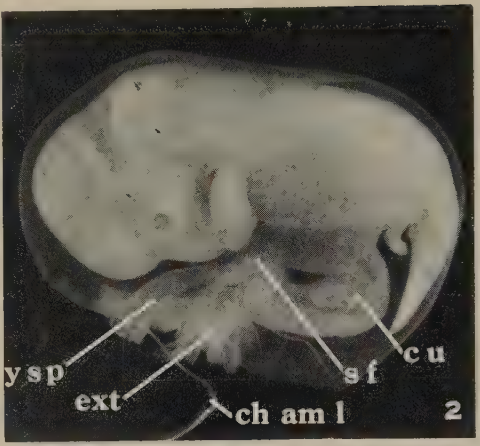
EMBRYO AND MEMBRANES OF THE HUMPBACK WHALE

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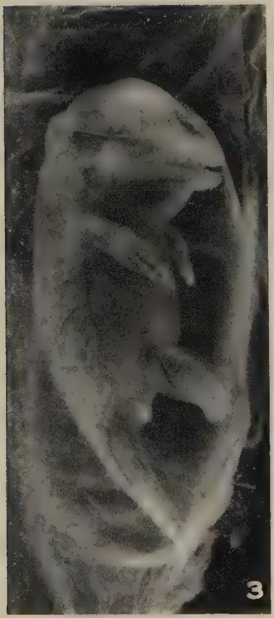

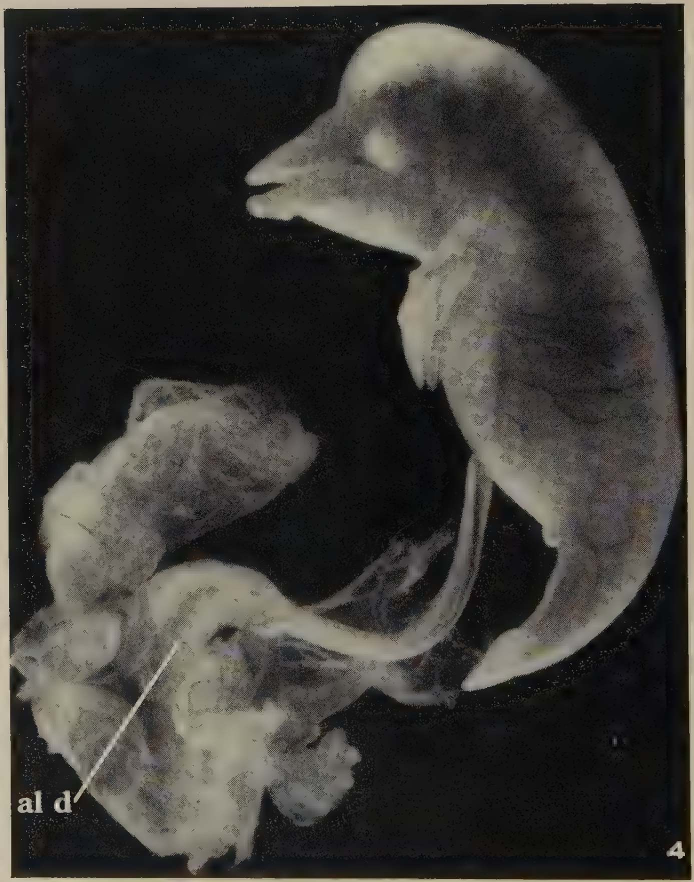

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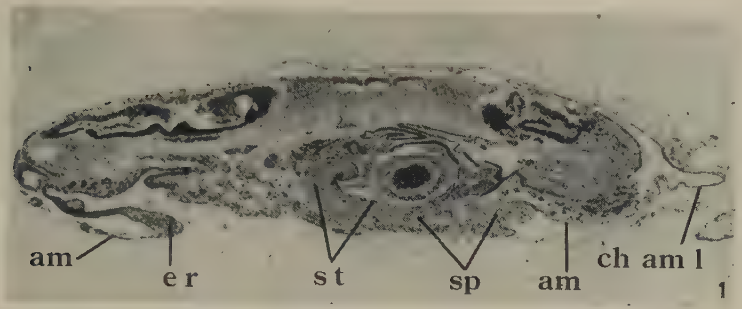
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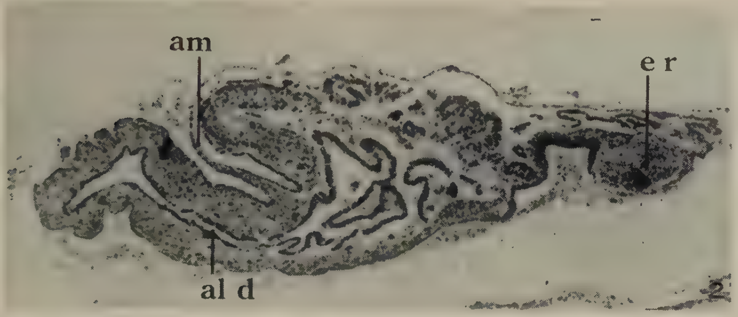

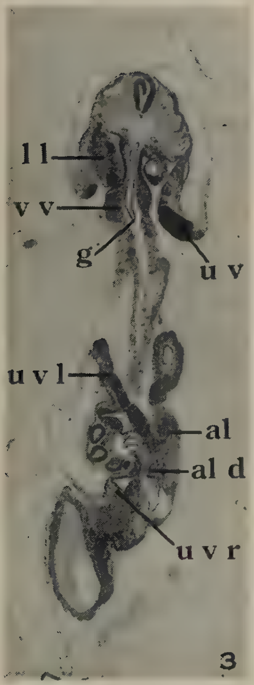
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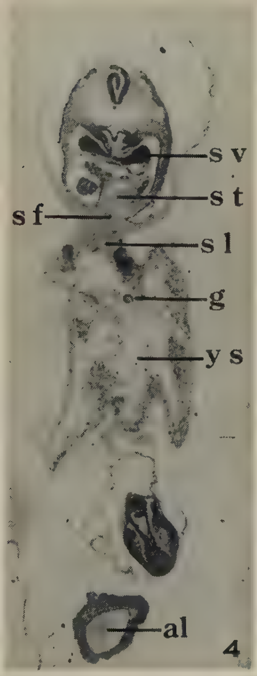
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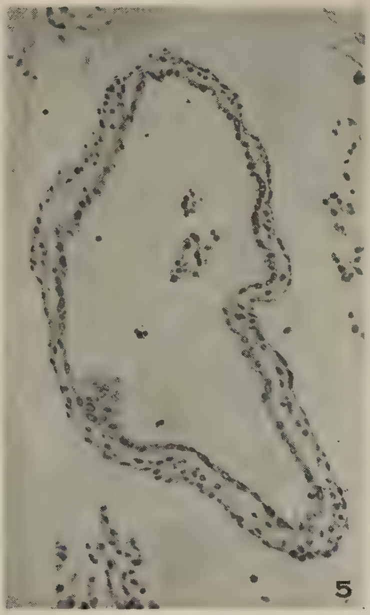

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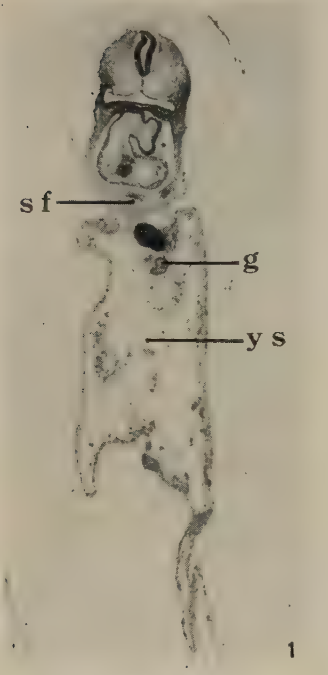

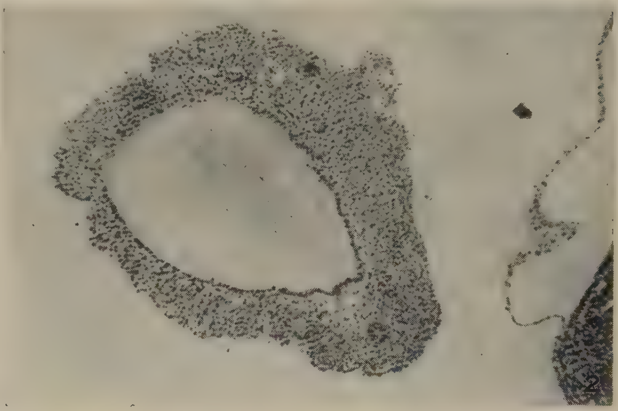

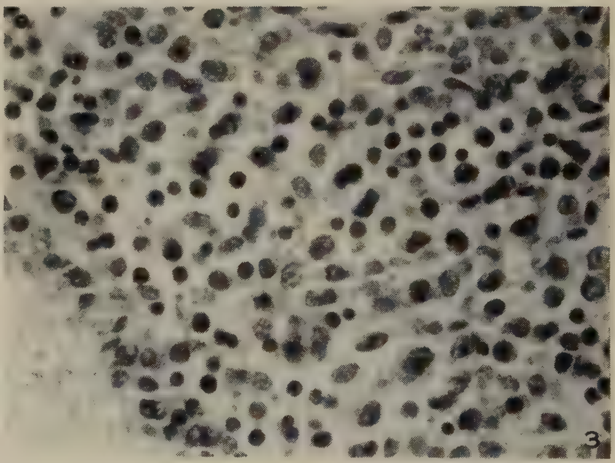

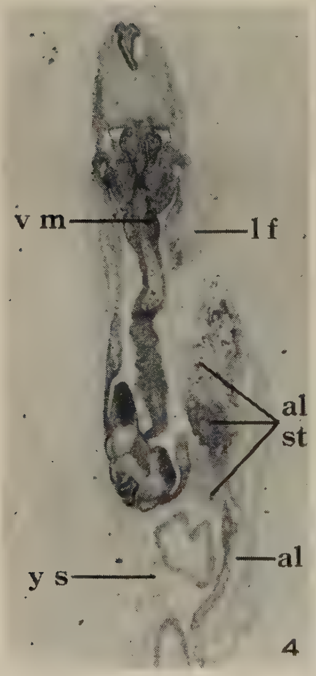
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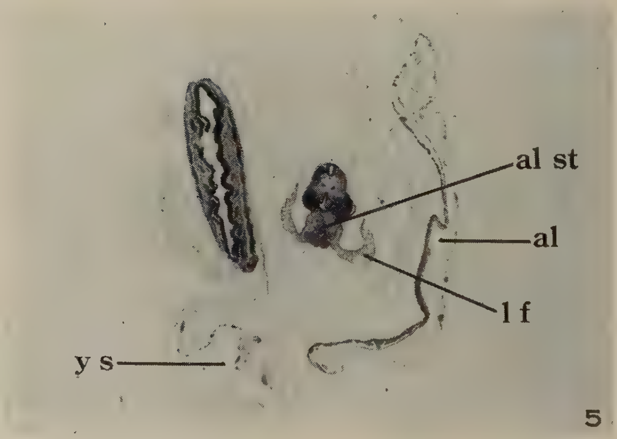
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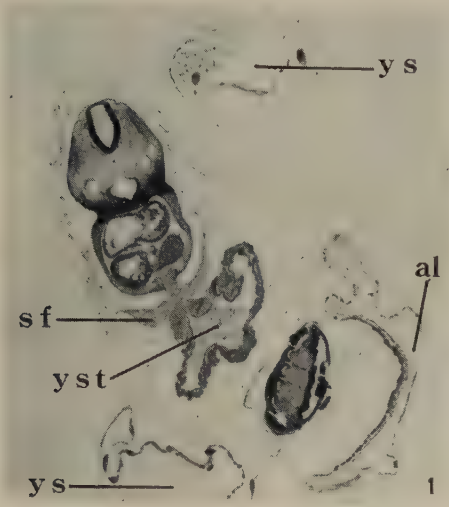
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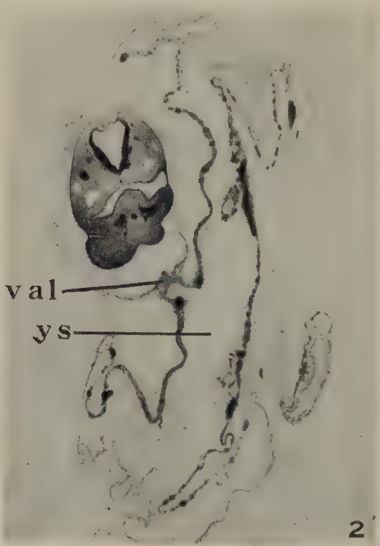

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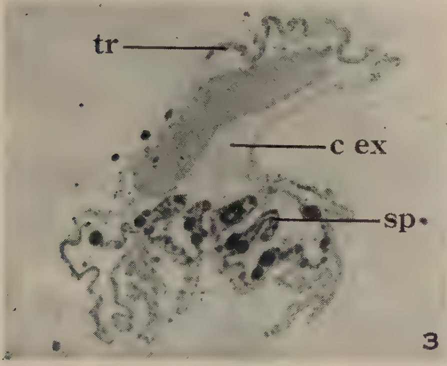

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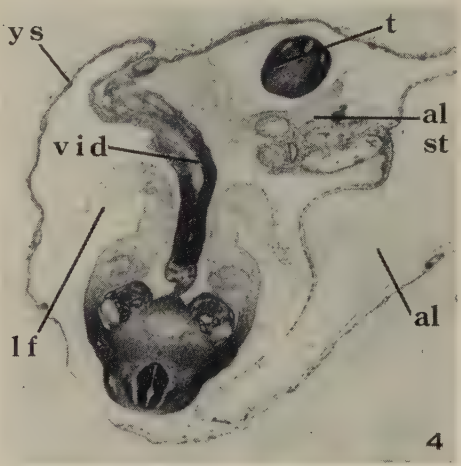
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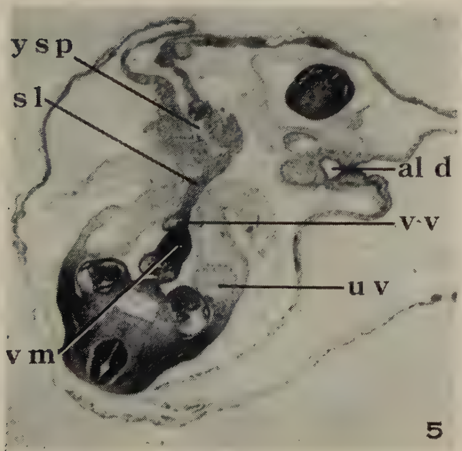
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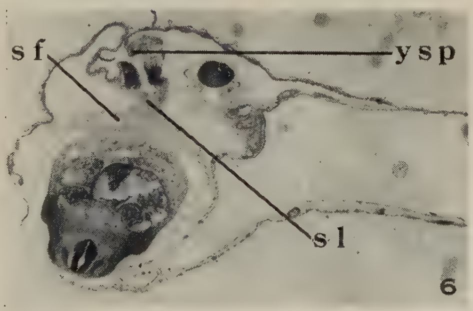

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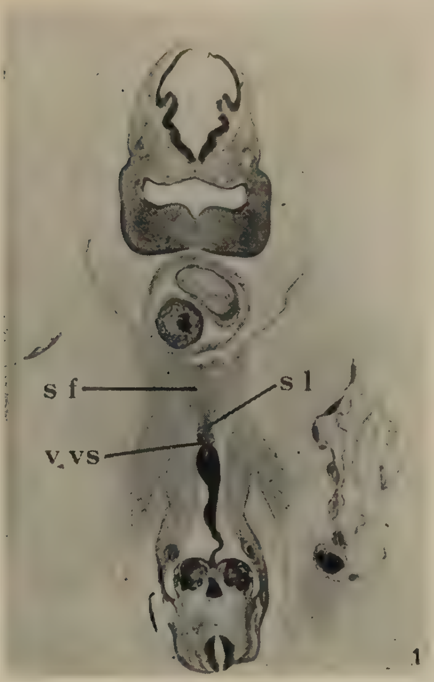

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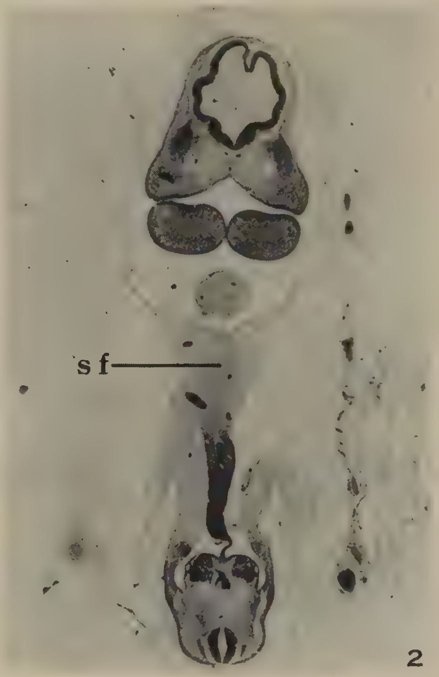

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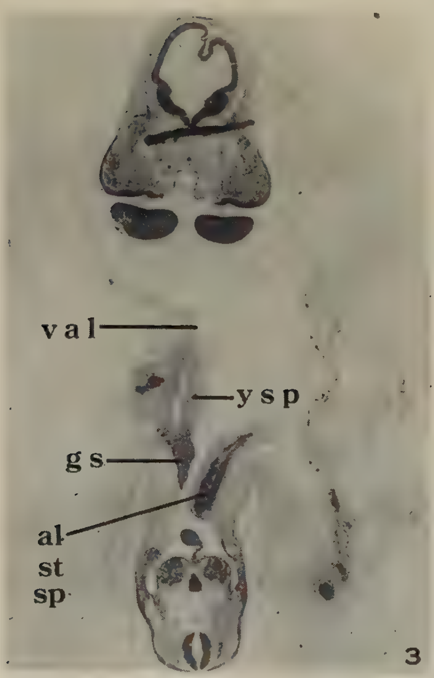
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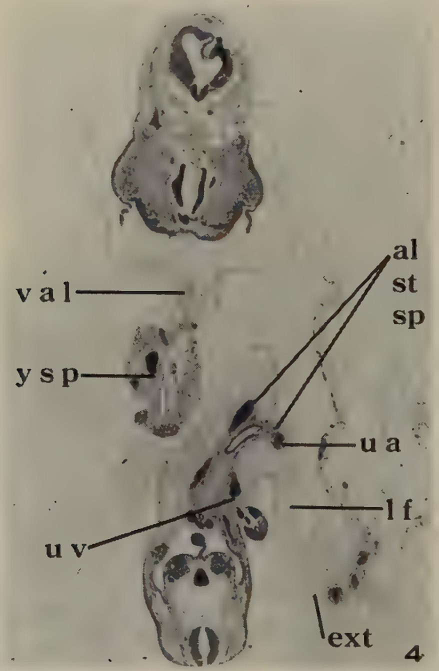
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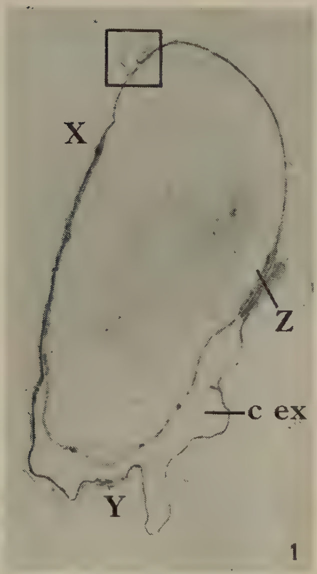

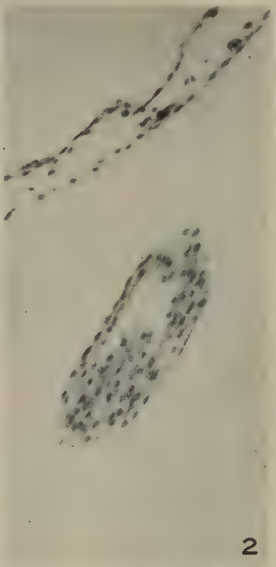

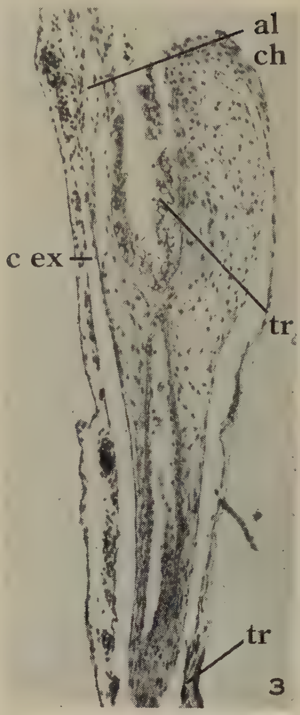
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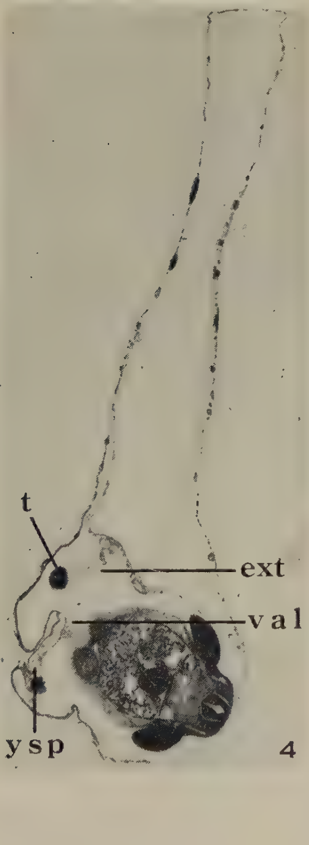
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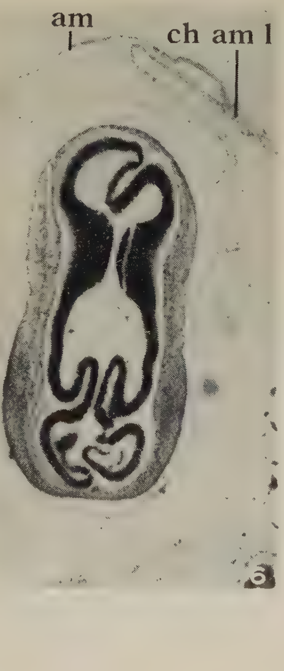

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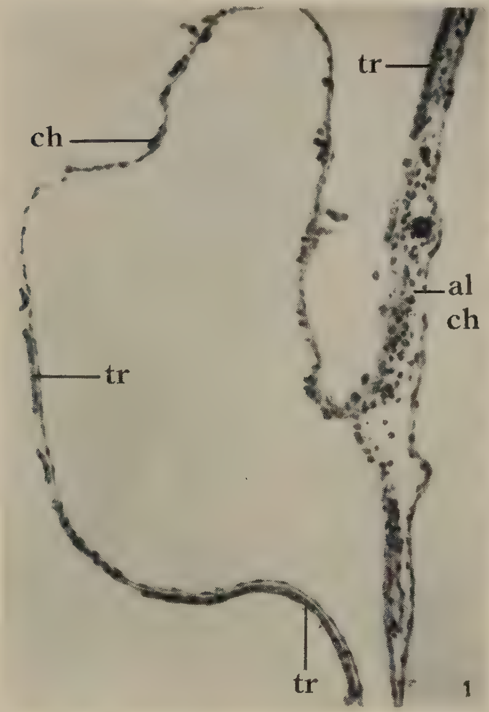
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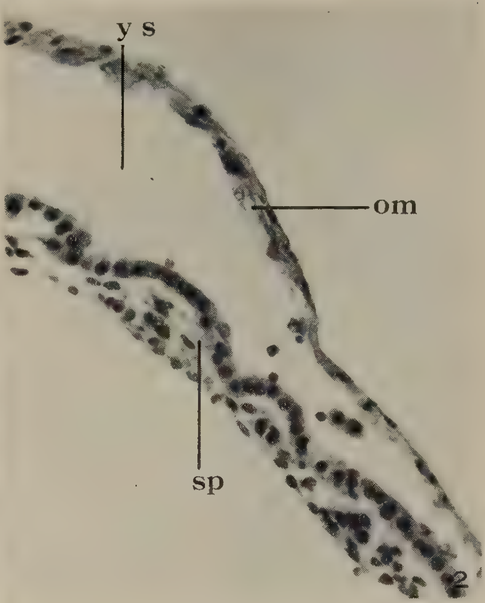

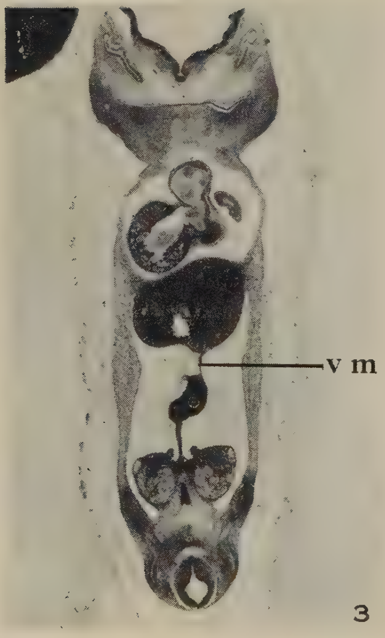

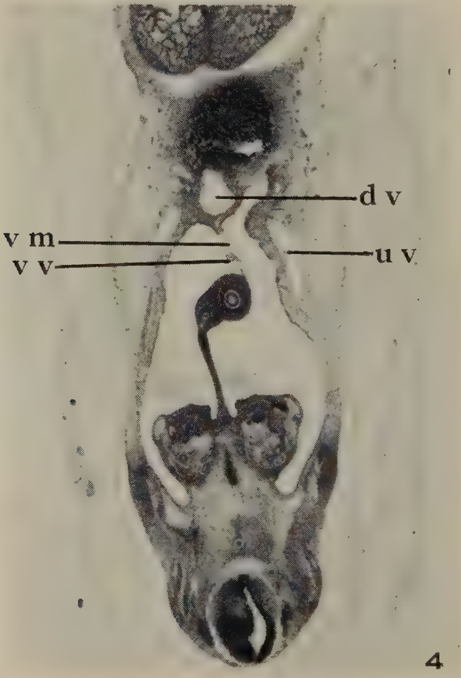

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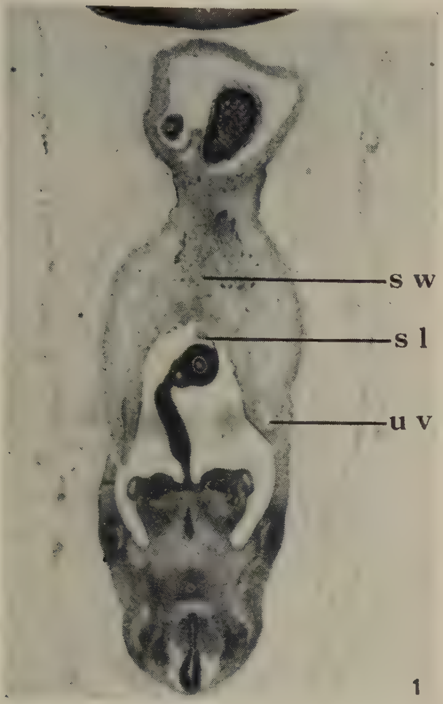

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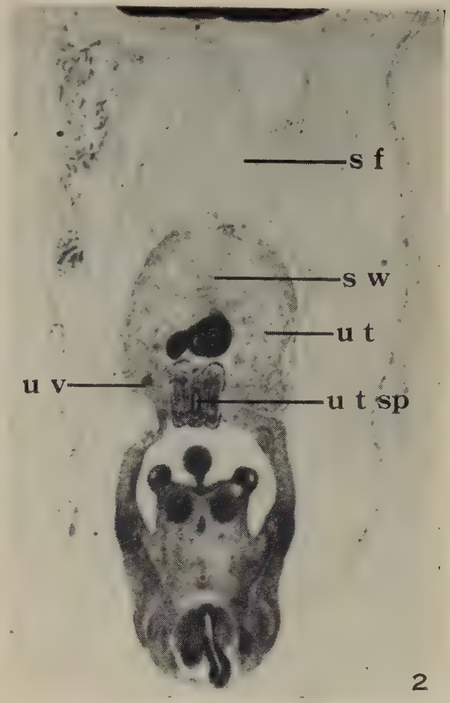
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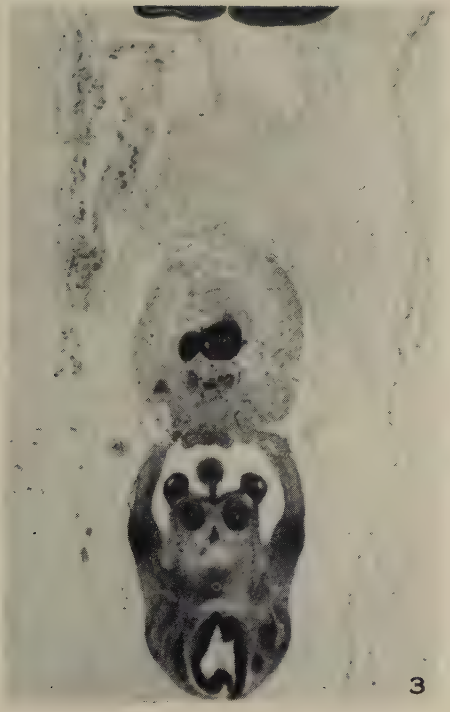

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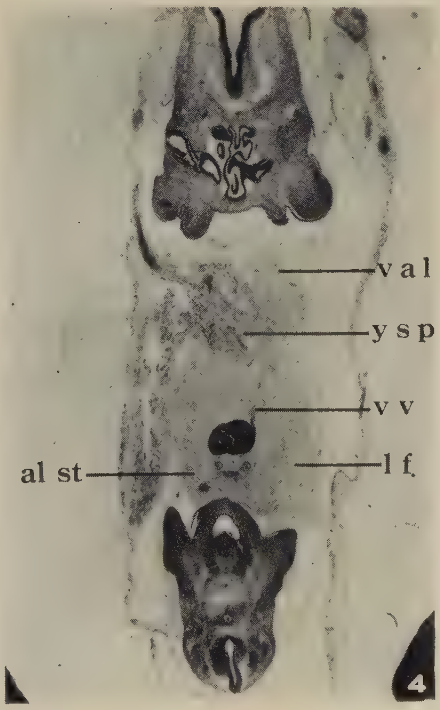
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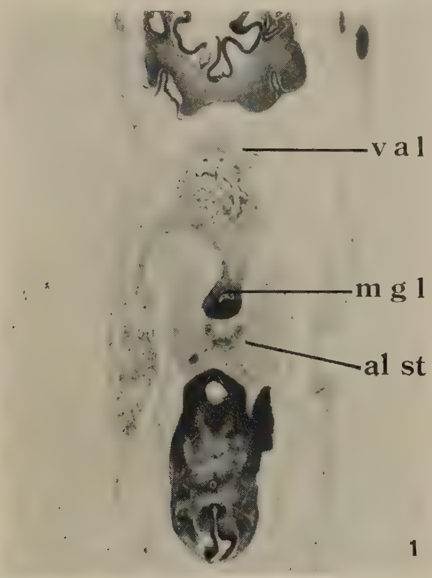
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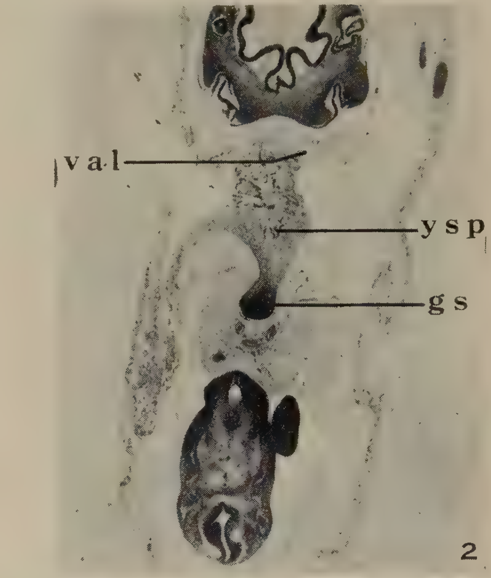

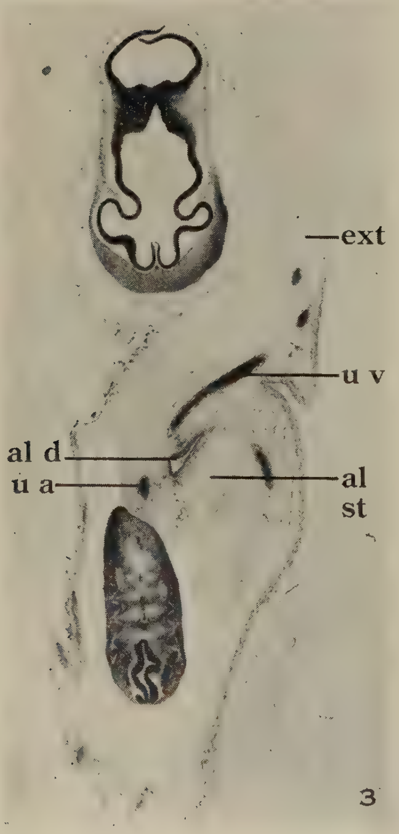
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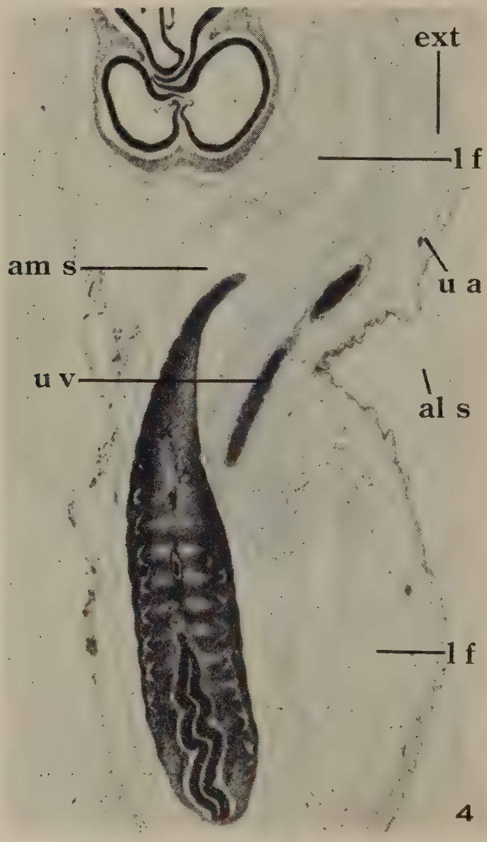
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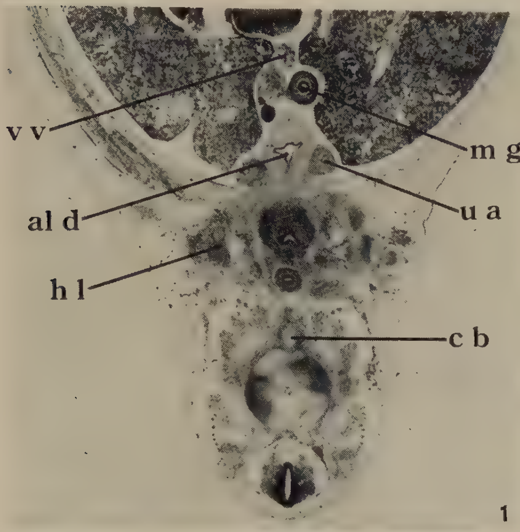
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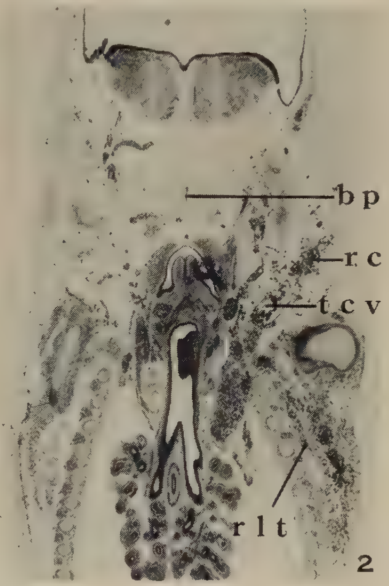
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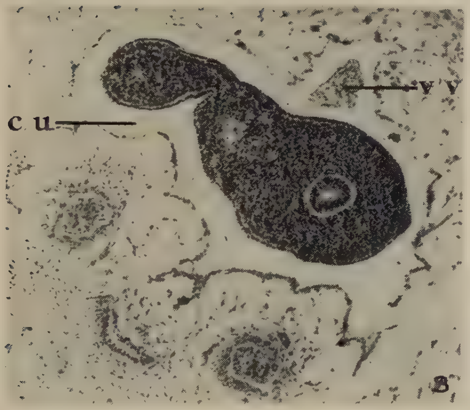

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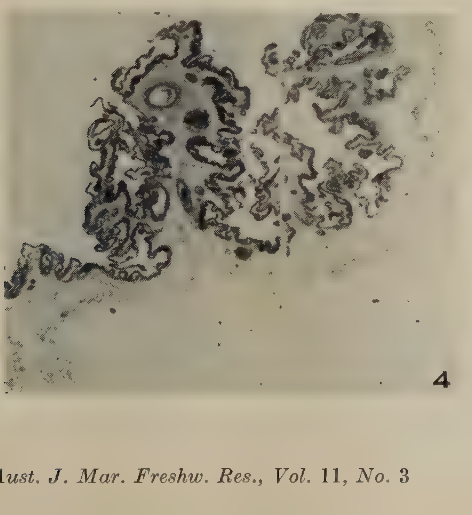

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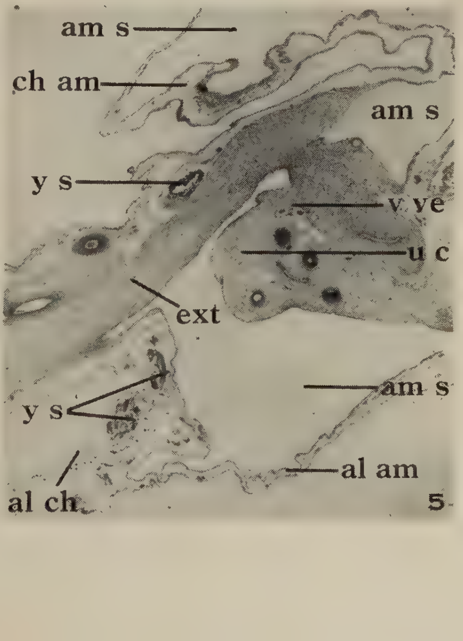
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